

THE FISHERIES BIOLOGY OF THE
TASMANIAN STOCKS OF
HALIOTIS RUBRA.

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Submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy in Zoology.

University of Tasmania
Hobart
March 1989

Except as stated herein, this thesis contains no material which has been accepted for the award of any other degree or diploma in any university, and, to the best of the author's knowledge and belief, this thesis contains no copy or paraphrase of material previously published or written by another person, except where due reference has been made in the text.

A handwritten signature in blue ink, appearing to read "J.D. Prince". The signature is stylized, with the first letters of the first and last names being capitalized and prominent.

J.D. Prince

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ABSTRACT

The fishery for *Haliotis rubra* or blacklip abalone is Tasmania's most valuable fishery, with a landed value of approximately \$50 million in 1988. Despite the fact that catch rates have remained relatively stable since 1970, commercial abalone divers in Tasmania are expressing grave doubts about the long term sustainability of this fishery. The aim of this study was to document the biology of *H. rubra* and the nature of the fishery in order to re-assess the fishery biology of this species, and current methods of stock assessment.

For this purpose, a broad ranging study of the structure and dynamics of the pre-recruit, and recruited, abalone populations has been completed. The ramifications of the results of this study have been explored using a model which simulates the dynamics of a single unit stock of abalone. Finally, in the light of these results I have re-assessed historical trends in catch per unit effort within the Tasmanian abalone fishery.

These results show that the structure of *H. rubra* populations is more dynamic than generally recognized, with high levels of recruitment and mortality amongst juveniles. Juveniles are cryptic, emerging onto the surface of the reef where they are vulnerable to commercial exploitation, as they mature. The emergent adult population is relatively stable being characterized by lower levels of growth and mortality.

On a spatial scale of 10-100 m the adult population is relatively mobile, exhibiting patterns of movement which could lead to aggregation and dispersion in response to changes in population pressure. In contrast the scale of larval dispersal is apparently restricted to 10's of meters. These results suggest that the scale of a unit stock in this species can be measure on the scale of 100's of meters and explain the spatial heterogeneity which is characteristic of abalone stocks.

Commercial divers have a high degree of knowledge about the spatial distribution of abalone and target known aggregations of stock. Divers allocate their effort according to a range of priorities, one of which is the expected catch

rate. When this characteristic of the fishery is combined with the biology of the species it is apparent that, on the spatial and temporal scale of commercial catch and effort data, catch rate is unlikely to be a reliable index of stock abundance.

A re-assessment of the catch per unit effort data confirms the conclusion, that a wide range of factors determine catch rate trends in the commercial fishery. For this reason standard methods of stock assessment are not applicable to the fishery. Developing new techniques of stock assessment and management, based on survey data and detailed knowledge of the relationship between stock and recruitment offers the best long term hope for managing this fishery.

CHAPTER 1

INTRODUCTION TO A STUDY OF THE FISHERY

BIOLOGY OF THE TASMANIAN STOCKS

OF *HALIOTIS RUBRA*.

1.1 INTRODUCTION

Haliotids, or abalone as they commonly known, are herbivorous marine archaeogastropod molluscs which inhabit shallow (0 - 35 m) reef environments around the major continents of the world and many of the islands in the Atlantic, Indian, Pacific and Southern Oceans. Haliotids are characterized by a row of rounded shell perforations (respiratory pores) overlying the respiratory cavity and their auriform shell morphology (Cox 1962). The fleshy foot, and bowl-like shell, of the larger species of abalone have been exploited by artisanal fishermen around the world for at least 6 000 - 7 000 years. For these people, the abalone they gathered in the intertidal, and shallow subtidal zones, provided food, utensils, tools and jewellery (Cox 1962; Sinclair 1963; Tegner in press). In the 20th century the world's stocks of abalone have been exploited primarily for the meat, although a less important market also exists for the shell which is mainly used for inlay. About one quarter of the 75 living species are large enough to be fished commercially (Mottet 1978). Catching methods are extremely simple (and have probably changed little during the centuries of exploitation); abalone are found by sight either by divers, or from the surface and prized or hooked off the rocks to which they attach (Cox 1962; Tegner in press).

Commercial fisheries for abalone exist in British Columbia, Korea, Oman, Philippines, South Africa, Australia, California, Japan, Mexico and New Zealand; the latter five being the major producers. Most abalone products are sold to Asian markets in Japan, Hong Kong, Taiwan and California. In recent years, the world's annual landing of abalone species has been about 14 000 - 20 000 tonnes (FAO 1984). While this tonnage contributes little to the total world fish catch, the fact that abalone are a luxury food and attract a high unit price means that fisheries for abalone are often relatively valuable to local economies (Harrison 1986).

During the 1970s and 80s Australia has consistently produced 25 – 50% of the world's supply of abalone and the abalone fishery is the third most valuable fishery in Australia (Harrison 1986). The Australian fishery exploits three species (Shepherd 1973), with the blacklip abalone (*Haliotis rubra* Leach) being the most important (Ward 1986). In Australia abalone are taken in depths down to

approximately 35 m by skindivers using compressed air equipment.

The development of the abalone fishery in Tasmania and in Australia has been described by Harrison (1969, 1983, 1986). Prior to 1960, the abalone stocks of Tasmania were relatively unexploited; the only harvesting that occurred prior to this time being by Tasmanian aboriginals, Chinese immigrants and some early settlers. During the 1960s with the growing popularity of SCUBA diving and the recognition of the Asian market, the fishery expanded rapidly. The early fishery was dominated by part-time participants working out of the major population centres. In 1969, the Tasmanian Government acted to control this expansion and restricted the fishery to 125 full-time professional divers. The industry is now fully professional with participants being highly skilled and strongly committed to the long-term future of the industry. In 1987 entitlements to the limited number of licenses were changing hands for between \$A850 000–\$A900 000. The abalone industry is Tasmania's most valuable fishery with a landed value of approximately \$A40 million in 1987. The Tasmanian catch is approximately 50 - 70% of the Australian catch and Tasmania is the largest single producer of abalone in the world (Ward 1986). Only two species of abalone are caught in Tasmania and blacklip abalone forms over 95% of the catch. The bulk of the catch is canned in Tasmania before going to the Japanese market (Harrison 1983).

The world's annual catch of abalone has been declining since the peak catch of approximately 28 000 tonnes in 1968; in 1983 the reported landing was approximately 14 000 tonnes (FAO 1963-84). The decline of abalone catches has been a widespread phenomenon causing concern amongst the managers of virtually all the world's abalone fisheries (Mottett 1978). It is widely accepted that abalone fisheries are highly susceptible to overfishing, a fact variably attributed to low growth rates, the low productivity of stocks, the sedentary nature of abalone, the high efficiency of fishermen, the natural variability of recruitment and recruitment overfishing (Breen 1986; Harrison 1986).

In the early 1980s, commercial abalone divers began expressing concern over the state of the Tasmanian stocks of abalone. This prompted the government instrumentality, which became the Tasmanian Department of Sea Fisheries, to conduct an assessment of the stock, based on catch and effort data (Harrison 1983), review management procedures, and initiate this study. The objective of this study

was to investigate the biology of *Haliotis rubra* as it pertains to the fishery, so that the methods used to assess and manage the abalone stocks could be developed and refined.

Despite being the most significant species in the Australian abalone fishery, relatively little had been published on the biology of *H. rubra* prior to this study commencing in 1984. A broad outline of its biology and ecology with particular relevance to South Australian conditions had been described by Shepherd (1973) while basic studies of growth, mortality, reproductive biology and habitat selection have been published by Harrison and Grant (1971), Shepherd and Laws (1974), Witherspoon (1975), Beinssen and Powell (1979), Shepherd *et al.* (1982), Shepherd and Hearn (1983), McShane *et al.* (1986). In his review of abalone biology and fisheries in Australia, Ward (1986) noted the paucity of research into this species and stressed the need for more biological research.

Gulland (1977) discusses the importance of broad biological studies as a basis for understanding the fisheries biology of a species and notes that "*in any given situation it is not easy to predict what piece of information is likely to be of greatest help in understanding the population dynamics of the stocks of fish concerned*". This study began with the objective of studying the general biology of *H. rubra*, both within the pre-recruit and post-recruit phases of its life cycle. In this context the word 'recruitment' has the normal meaning within fisheries science (Gulland 1969) indicating recruitment to the fishery, or the process by which exploited species become vulnerable to the fishery.

At this point it is important to clarify the two main ways that this word is used within the fields of fisheries and marine biological science. Within fisheries science the meaning of 'recruitment' is as above, but this is distinct from its meaning within the broader field of marine invertebrate biology. In that context it means recruitment to the total population, the process by which newly settled individuals metamorphose and join the youngest age class of juveniles (Connell 1985). Through the course of this thesis it will be necessary to use both meanings of this term and I will clarify the manner in which I am using the word at each point of this study.

An examination of the literature dealing with the fishery biology of haliotids shows that three recurrent and unresolved issues receive considerable attention.

These are the structure and ecology of haliotid populations, the scale and structure of unit stocks, and the nature of the relationship between catch rate and stock abundance. Consequently within the overall framework of a general study of the biology of *H. rubra* particularly attention has been given to these specific areas.

1.2 THE STRUCTURE AND ECOLOGY OF HALIOTID POPULATIONS

The structure and ecology of the natural population of an exploited species is an important part of the fishery biology of a species. Qualitative knowledge about a natural population's structure and ecology forms a major part of the detailed biological information which may lead to a better understanding of a species population dynamics (Gulland 1977). Quantitatively, the productivity of a fished stock is determined by the same parameters that result in the structure of the population: recruitment, growth and mortality (Beverton & Holt 1957). Obviously, a dynamic population with high levels of recruitment, growth and natural mortality, will be more resilient to fishing pressure than a population with low levels of recruitment and long lived, slowly growing individuals.

Abalone populations have generally been found to be characterized by strongly skewed size frequency distributions dominated by accumulations of older individuals, small numbers of sub-adults and almost no recent recruits, and this population structure is accepted as 'typical' for abalone (Tegner in press). The small number of juveniles found in the natural environment has restricted the scope of research into the structure of natural abalone populations, and studies of juvenile abalone have generally concentrated on growth and the timing of recruitment. This adult dominated population structure and the limitation it imposes on research is a common feature of studies of marine molluscan species (Yamaguchi 1977; Jensen 1981).

We know, largely from laboratory studies, that abalone larvae settle preferentially onto the surfaces of encrusting coralline algae (Shepherd & Turner 1985) where they feed on the algal cuticle and bacterial biota (Garland *et al.* 1985). Juvenile abalone are cryptically coloured and, after moving off the coralline surfaces, continue living beneath the boulder substrate on which the adults are commonly found. Abalone emerge from the cryptic habitat and become vulnerable to divers as they increase in size (Shepherd 1973; Witherspoon 1975). The preference that small

abalone together with many other species of marine invertebrates, have for cryptic habitats makes them extremely difficult to sample (Sarver 1979).

Consistent with the accepted population structure for abalone, and in the absence of evidence to the contrary, it has been assumed that the instantaneous rates of mortality for juvenile abalone are low, similar to those of the adults, (Sainsbury 1982a; Shepherd *et al.* 1982; Fournier & Breen 1983) and that populations are relatively static with little recruitment and low rates of turnover (Clavier & Richards 1986a). However, Hines and Pearse (1982) observed a stable population of abalone sustaining a high level of predation by sea otters and estimated an annual turnover of 92%. This level of turnover is inconsistent with the published estimates of mortality and the accepted population structure for abalone. Consequently Hines and Pearse postulated that the mortality rate for small abalone is much higher than that of larger animals and that abalone populations are very productive, with high rates of turnover.

1.3 THE SCALE AND STRUCTURE OF UNIT STOCKS

In fisheries biology it is important to accurately delimit the area occupied by a 'unit stock' (Gulland 1969) as the assumption of a single, completely self-contained, homogeneous stock or 'unit stock', is fundamental to the application of most fishery models (Russell 1931). Despite the necessity of making assumptions with regard to the scale of a unit stock the subject is relatively unstudied and unresolved for abalone.

The scale of a unit stock is a function of the mobility of the adult, juvenile and larval phases of an organism (Hancock 1979). In abalone, the mobility of the juvenile and adult phases has been reasonably well documented. Most studies have found the movement of adult and juvenile abalone to be relatively restricted. Beinssen and Powell (1979) studying a population of *H. rubra* in Victoria (Australia), found that over a 2 year period only 8% of the tagged animals moved more than 40 m, a similar scale of movement has been observed for this species in Tasmania (R. White & P. Whyte, pers. comm.). This scale of movement is also consistent with published data for most of the other species that have been studied (Poore 1972a; Clavier & Richard 1984; Shepherd 1986a). Newman (1966), studying the South African species *H. midae*, found slightly greater movement patterns; over a period of 6-18 months 56% of the abalone he recaptured moved in

excess of 40 m, the greatest distance moved being approximately 360 m. Ault and Demartini (1987) also found that abalone moved frequently with some abalone moving in excess of 400 m.

Knowledge of larval dispersal is extremely restricted and, prior to this study, no information on the dispersal ability of haliotid larvae had been published. From observations made under laboratory conditions it has generally been assumed that the lecithotrophic haliotid larvae are pelagic and disperse widely (Mottett, 1978; Fedorenko & Sprout, 1982; Sluczanowski, 1984; Tegner & Butler, 1985a). Using this assumption, and the results of a drift bottle survey, Tegner and Butler (1985a) hypothesised that significant recruitment was unlikely to occur at distances >10–20 km from abalone populations; suggesting that the scale of unit stock is measurable in tens of kilometers.

Despite the paucity of information about the scale of unit stocks, those involved with the management of these fisheries have often assumed they were studying unit stocks so that they could apply standard methods of stock assessment. For example, Harrison (1983) modelled the entire abalone fishery of Tasmania, as well as smaller statistical blocks as unit stocks. In a similar fashion, Breen (1986), while acknowledging that the abalone fishery of British Columbia probably consists of more than one stock, for the want of better information, modelled the fishery as a single unit stock.

1.4 THE NATURE OF THE RELATIONSHIP BETWEEN STOCK ABUNDANCE AND CATCH PER UNIT EFFORT.

It is rarely possible to measure the actual abundance of an exploited stock directly and, as a consequence it is more usual for an index of abundance to be used. Many methods for estimating the potential yield of a stock use catch per unit effort (CPUE) as an index of stock abundance (Gulland 1977), and the assumption that CPUE reflects stock abundance is probably the most fundamental assumption in the field of fisheries biology. It is widely recognised that this assumption is not always valid; for example Paloheimo and Dickie (1964) have documented the difficulty of using this approach for schooling fish. Likewise Hancock (1979) has cautioned that the catchability of many invertebrates is extremely variable so that CPUE can be an unreliable index of invertebrate stock abundance, while Hilborn and Walters (1987)

have presented evidence suggesting that this assumption may be violated in spatially heterogeneous fisheries.

The relationship between CPUE and stock abundance in abalone has also been discussed in the literature. Harrison (1983, 1986) and Breen (1986) have suggested that several factors may effect this relationship, these are:

- changing diver efficiency, due to learning, improvement of equipment and technique, and competition amongst divers (Harrison 1983; Breen 1986);
- the progressive discovery and exploitation of sedentary beds of abalone (Harrison 1983);
- and variation in catchability associated with different bottom types (Harrison 1986).

However with the exception of Beinssen (1979), who measured the fishing power of divers, little research has been conducted into this aspect of the fishery biology of abalone.

1.5 THE STRUCTURE OF THIS STUDY

The unresolved nature of the central issues means that any study of abalone fisheries biology must address them. Consequently, these topics underlie this study. Chapters 2 and 4 are basically broad biological studies of the population structure and dynamics of *H. rubra*. Chapter 2 concentrates on the abalone population during its cryptic phase, while it is hidden within the boulder substratum and relatively invulnerable to fishing pressure, whilst Chapter 4 examines the part of the population which has emerged from the cryptic habitat and become vulnerable to exploitation.

Chapter 3 describes a series of experiments which were suggested by the techniques developed during the study described in Chapter 2, as well as qualitative observations made during that study. These experiments were conducted as an attempt to test experimentally the likely scale of larval dispersal.

In an attempt to address the issue of how CPUE relates to stock abundance Chapters 5-7 concentrate extensively on the interaction between the biology of *H. rubra* and the fishery for this species. Chapter 5 describes a Leslie-Delury type fishdown experiment that I conducted in order to document basic facets of the fishery dynamics in this industry. In Chapter 6 these details are combined with the

basic biology of *H. rubra* in a model of a single exploited abalone population which I built as a means of drawing the diverse threads of this study together, and to explore their ramifications. I present the history of the Tasmanian abalone fishery in Chapter 7 and, in particular, examine the CPUE data for this fishery attempting, in the light of the preceding chapters, to explain the observed trends.

In my brief concluding chapter I have tried to go beyond summarizing and re-iterating the major findings of this study. I propose a direction for future research into the fishery biology of *H. rubra*; a direction which, on the basis of this study, could be expected to lead to the development of techniques necessary to successfully manage this fishery.

CHAPTER 2

THE DYNAMICS, STRUCTURE AND GENERAL

BIOLOGY OF A PRE-RECRUIT POPULATION

OF *HALIOTIS RUBRA*.

2.1 INTRODUCTION

Abalone populations have generally been found to be characterized by accumulations of long lived adults, small numbers of sub-adults and almost no newly settled abalone (Tegner in press.). Consistent with this population structure, it has been assumed that the instantaneous rates of mortality for juvenile abalone are low, similar to those of the adults, (Sainsbury 1982a; Shepherd *et al.* 1982; Fournier & Breen 1983) and that populations are relatively static with little recruitment and low rates of turnover (Clavier & Richards 1986a).

The aim of this segment of the study was to examine the structure and biology of the pre-recruit population in more detail to test the hypothesis that haliotid populations have low, sporadic levels of recruitment, low, constant mortality, and are dominated by older individuals.

2.2 MATERIALS AND METHODS

2.2.1 Description of Study Site

The study area at Blubber Head in Port Esperance, Tasmania (43°19' S, 147°04' E) is a uniform section of rocky coastline extending approximately 70 m from high water mark to a depth of 11 m. The bottom is principally composed of three layers of boulders resting on silt, although in some areas the underlying substratum is solid rock. The boulders are of irregular shape and are mostly 30 to 40 cm in length and 10 to 20 cm in depth and breadth.

The macroalgal community of the area is typical of a furoid association indicative of slight to moderate wave action (Sanderson & Thomas 1987). Some compression of the floral zones is evident at the site which is probably caused by tannin-stained freshwater influence from the nearby Esperance River reducing light levels (C. Sanderson, pers. comm.). The shallow region (0 to 5 m) is dominated by *Durvillaea potatorum* (Labill.) Aresch. and *Xiphophora* sp., particularly down to 1m. Below 1m, the algal assemblage is more heterogeneous and principally includes *Phyllospora* sp., *Acrocarpia paniculata* (Turn.) Aresch., *Cystophora moniliformis* (Esper), Wom. and Niz. and *Sargassum bracteolosum* (Mertens) C. Agardh. The algae *Lessonia corrugata* Lucas, *Perithalia* sp. and *Macrocystis*

pyrifera (L.) C. Agardh are also present but they are less abundant. The algal assemblage below 5 m is depauperate with <20% algal cover. The main macroalgal species in this region are *A. paniculata*, and species of *Ecklonia*, *Phyllospora*, *Thamnoclonium*, *Peyssonnelia*, *Zonaria* and encrusting coralline algae.

2.2.2 Sampling Technique

I developed a novel method of sampling abalone populations which proved to be particularly suited for the Blubber Head site. Details of this technique's development and relative performance are published in Prince and Ford (1985). Copies of the material published in refereed journals during the course of this study are contained in Appendix 1. Initial surveys of the site (February 1984 and June 1984) revealed that the abalone were most abundant at depths <4 m and that the size composition of the abalone population was extremely variable over small distances (20 to 40 m). After these initial surveys the abalone were sampled at 4-monthly intervals commencing in October 1984. Sampling took place at four points approximately 50 m apart along the shoreline, these points were marked to ensure consistency.

A boat was anchored directly in front of each marker and 11 m² was selected at each point, for sampling, by throwing 1 m² quadrat from the boat. If the quadrat landed on an area where the boulders were too large to collect, or the substratum was entirely sand and silt, or if the square landed in more than 4 m depth, the square was retrieved and re-thrown. From each selected area a diver collected all the substratum material possibly suitable for abalone, principally boulders and kelp. The few boulders too large to lift to the surface were searched underwater and all abalone collected.

The substratum material was placed in bins and bathed in a 1% solution of ethanol in sea water for a minimum of 10 min. This material was then brushed with a soft brush before being removed from the solution. After all the boulders removed from a square had been soaked, the contents of the bins were drained through 15 mm and 0.5 mm sieves. Abalone retained by the coarser sieve were collected and the sample held by the smaller sieve was returned to the laboratory for examination. These samples were washed through sieves of 9, 4, 2 and 1 mm aperture and the extracted abalone were preserved. The maximum shell length of all abalone

collected was measured for to the nearest millimetre.

2.2.3 Analysis of Length Frequency Data

The Mix program (Macdonald & Green 1985) was used to decompose the length-frequency data. The program fits a series of normal curves to a multimodal length frequency distribution, estimating the mean and standard deviation of each component distribution and the proportion of the sample represented by each component curve.

For this analysis, the data from the four sampled points were pooled. The February 1984 sample was not analysed because of its small size. The low abundance of larger abalone in the samples prevented the Mix model from converging on any unique description of the larger size classes. To enable the estimates of the model to converge it was necessary to truncate the data sets and use only the more abundant smaller size classes. The samples were truncated at 80 mm except for the June 1984 histogram which was truncated at 40 mm because only 20 quadrats were sampled. Using the truncated data sets the Mix model converged on a unique set of estimates for all data sets excepting the October 1984 sample. For this sample no unique solution could be found so trial and error was used to obtain the best fit for the data.

2.2.4 Growth

Growth in abalone <80 mm was examined by following the progression of the modes described with the Mix model within the truncated length frequency data. The growth of larger individuals was examined using growth increment data collected from a tagging program. Between January 1983 and February 1985 705 *H. rubra* were tagged and released at the sample site. Two tagging techniques were used: small laminated tags glued to the shells of the abalone with fast setting glue and disc tags riveted to a respiratory pore of the abalone. A total of 646 were tagged with the former technique and 59 with the latter. Animals representing the size range 34 to 126 mm were released. Recapture of released abalone took place during August and September 1986.

The methods of Fabens (1965) were used to analyse and describe the growth parameters of the abalone population. The Fabens method fits a von Bertalanffy

growth curve to tag return data estimating the values of K and L_{∞} . The non-linear least-squares algorithm LMM1 modified by Dr A.J. Miller from Osborne (1976) was used to fit the data.

2.2.5 Mortality

The length-frequency histograms were re-analysed with the Mix model. In this second analysis the mean lengths and standard deviations estimated using the Mix model and the truncated data sets were held fixed. The growth patterns described by the growth study were used to estimate the mean size of the >80 mm age classes present in the population and a fixed standard deviation for these distributions was estimated on the basis of the preliminary analysis. These parameters were then held fixed while the Mix model was allowed to converge on new estimates of the proportion of abalone in each size class. The results of this analysis were used to estimate the density of the year classes. The initial sample collected in February 1984 has been excluded as depths >4 m were sampled on that occasion.

Estimates of the instantaneous rate of total mortality (Z) were made by regressing the natural logarithm of density against age (Beverton & Holt 1957).

2.2.6 Breeding

Samples of approximately 20 abalone from each 10 mm size class >60 mm were collected for breeding studies in July 1986. After fixation in 10% formalin the visceral mass was sectioned beneath the visceral coil and the cross section placed against clear plastic and drawn. The relative areas of gonad and digestive gland in the cross section were calculated by weighing the plastic outlines. A gonad index was calculated as the percentage of the area of the cross section made up by the gonad. The gonads were also examined to ascertain whether yolked eggs were present. After the cross sections had been drawn the gonads of the female abalone were dissected from the digestive gland and gently teased apart into 50 to 250 ml of water. The water was agitated until the gonadic material was evenly dispersed, two or three 0.5 to 1.0 ml samples were then taken and examined for the presence of yolked eggs.

2.2.7 Size at Emergence

The size of abalone that had emerged from the sub-boulder habitat and were living on top of the boulder substratum in non-cryptic habitats (emergent abalone), and their relationship to the rest of the population, were examined in July 1986. A 60 m long section of shoreline was marked out by research divers and the density of abalone in the area measured by randomly selecting and sampling a total of $20 \times 1 \text{ m}^2$ quadrats. Research divers then spent a total of 46 diving-hours collecting all the abalone that could be found in the 60 m section of shoreline without disturbing the substratum. All abalone collected were measured to the nearest millimetre. After removing the emergent abalone, a further $20 \times 1 \text{ m}^2$ was sampled in order to measure the remaining density of abalone. Sampling was conducted using the anaesthetic technique of Prince and Ford (1985) described previously (v. 2.2.2).

2.3 RESULTS

2.3.1 Recruitment to the Population

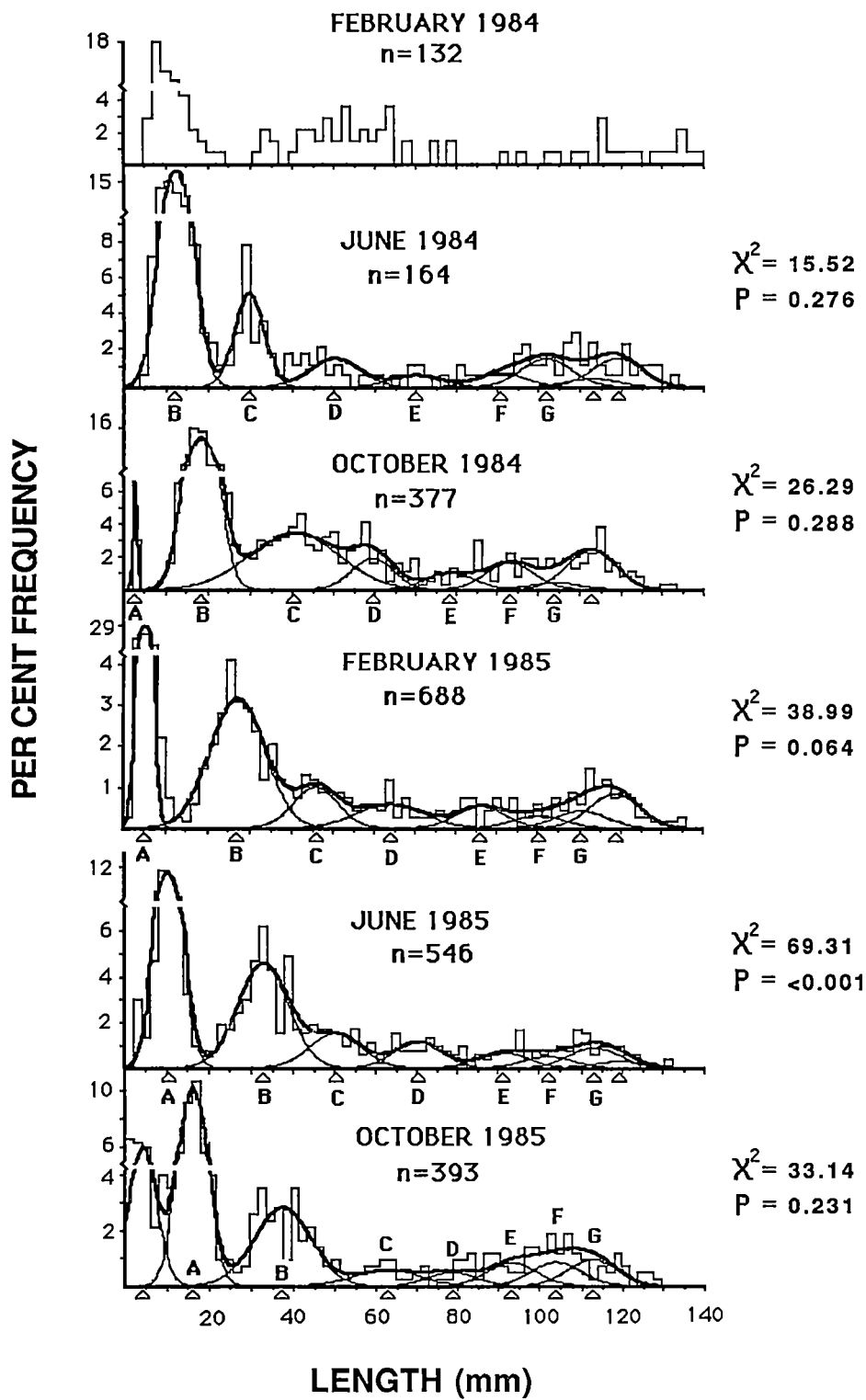
The smallest abalone sampled were 1 to 2 mm in maximum length, at which size they were in the process of forming, or had just completed forming their first respiratory pore. The results of laboratory studies of larval and early juvenile growth in *H. rubra* suggest that this size is reached at approximately 30 to 45 days post fertilization (J.F. Grant, pers. comm.).

Large numbers of recently metamorphosed individuals were found to have entered the population in October 1984 and 1985 (Fig. 2.1). In October 1984 this newly recruited class (recruited to the population) was detected at densities of 0.3 ab.m^{-2} . By February 1985 this age class had increased in abundance to 9.7 ab.m^{-2} indicating that recruitment to the population had continued during this period. A total of 130 abalone in the 3 to 4 mm size class were found in February 1985 along with only 18 abalone in the 1 to 2 mm size class indicating that the major period of recruitment occurred before February. However the fact that eight abalone $<4 \text{ mm}$ were also found in June 1985 indicates that some minor spawning and recruitment is possible at other times of the year.

The rate of recruitment over the two years of the study was relatively constant, with the density of new recruits measured in June 1984 approximating that measured in June 1985.

Figure 2.1

Length-frequency histograms for *Haliotis rubra* sampled at Blubber Head between February 1984 and October 1985; curves fitted using Mix model. Values of χ^2 and P refer to Mix analysis of <80 mm histograms. Thin lines: component distributions described by Mix. Thick lines: shape of component curves pooled. A-G: Individual year-classes identified by analysis.



2.3.2 Growth

2.3.2.a Analysis of Length Frequency Histograms

The size distributions described for the length frequency histograms (Fig. 2.1) by the 'Mix' model for each sample are detailed in Table 2.1. Five major size classes were described with the Mix model, the smallest size class observed during the study began recruiting to the population in October 1984 and will be referred to as mode A. Between October 1984 and February 1985 this size class increased in abundance indicating that recruitment to the population continued during this period. The next largest size class of animals observed (mode B) was first observed in June 1984 at a mean size of 12.4 mm. This size class was observed to increase in size to 37.8 mm by October 1985. The third size class (mode C) was observed to grow from 29.7 mm in June 1984 to a mean size of 63.7 mm in October 1985. The largest size class (mode D) described by the Mix model was observed to have a mean length of 60.6 mm in October 1984. This size class was observed until June 1985 when it had obtained a mean size of 70.2 mm.

At a nearby site I observed that a widespread spawning of *H. rubra* occurred during the last week of September (v. 3.3.1). On the basis of this observation, together with the observation that recruitment to the general population at Blubber Head generally occurs between October and February (v. 2.3.1), I have assumed an 1 October birth date for this population. Using this date, in February 1985 modes A, B, C and D can be estimated to have been approximately 4, 16, 28 and 40 months old respectively. A highly significant linear correlation ($p < 0.001$; $n = 16$; $r = 0.991$) exists between the means of the size classes (< 80 mm), described by the 'Mix' model, and age (Fig. 2.2). This relationship can best be described by the equation;

$$L = 20.83 A - 2.46$$

where A is age in years and L is length in mm.

2.3.2.b Tagging Study

A total of 55 tagged abalone were recovered during the recapture searches with the time at liberty ranging from 490 to 1 126 days. Nine of the abalone recaptured had been tagged with rivet tags. The tagged abalone were primarily from the larger

size classes. Approximately 50% of those recovered were released at a size >60 mm and over 85% of the animals recaptured were >90 mm when recovered. This was because of the difficulty of capturing, handling and tagging smaller abalone.

Table 2.1 Estimates, and their standard errors, of the mean lengths (mm), proportions (fraction of sample size) and standard deviations (mm) of the mean lengths contained in the 0-80 mm length-frequency histograms. The estimates were made using the 'Mix' model (Macdonald & Green 1985).

Sample Analysed	Mean		Proportion		Standard Deviation		No. n	No. Squares Sampled	Chi-Squared		
	est.	s.e	est.	s.e.	est.	s.e.			Value	d.f.	P
June 1984 0-40 mm	12.5	0.3	0.77	0.03	3.6	0.3	164	20	15.5	13	0.276
	19.7	0.6	0.23	0.03	3.4	0.5					
October 1984 0-80 mm	2.3	3.6	0.03	0.01	0.5	5.8	377	44	26.3	23	0.288*
	18.5	0.3	0.53	0.04	3.7	0.3					
	41.3	3.0	0.36	0.13	10.9	4.5					
	60.6	2.6	0.09	0.09	5.1	2.5					
February 1985 0-80 mm	4.8	0.1	0.62	0.02	1.5	0.1	688	44	39.0	27	0.064
	26.6	0.9	0.25	0.02	6.5	0.7					
	45.3	2.2	0.07	0.04	5.3	2.6					
	63.2	4.1	0.06	0.02	8.0	2.5					
June 1985 0-80 mm	10.3	0.2	0.47	0.02	3.1	0.2	546	44	69.3	28	<0.001
	32.7	1.2	0.34	0.05	6.0	0.9					
	50.2	2.8	0.11	0.06	6.2	3.1					
	70.2	2.0	0.08	0.03	5.8	1.4					
October 1985 0-80 mm	3.8	0.6	0.24	0.03	3.4	0.6	393	44	33.1	28	0.231
	16.0	0.4	0.42	0.03	3.3	0.4					
	37.8	0.9	0.27	0.03	6.9	1.0					
	63.7	2.7	0.07	0.02	7.4	2.0					

* Estimates of parameter values did not converge.

Analysis of the tag return data gave an estimate for the von Bertalanffy equation parameters K and L_∞ of 0.288 (s.e = 3.70 x 10⁻²) and 139.7 mm (s.e = 7.24) respectively.

The linear equation describing the growth of abalone <80 mm implies that the t₀

(the theoretical time when size is equal to zero) for this population is approximately 0.12 y. However if a t_0 of 0.12 y is used with the parameters estimated for the von Bertalanffy curve, the curve greatly over estimates the early growth described by the age-length data.

The growth of abalone in this population is best described by using both equations independently, describing the growth of <80 mm abalone in the area with a straight line and the growth of larger abalone with a von Bertalanffy curve. If 80 mm is accepted as the limit of both curves the straight line equation can be used to estimate an age of 3.98 y for an 80 mm animal. Substituting these values into the von Bertalanffy equation a t_0 of 1.01 y can be estimated for use with the von Bertalanffy section of the curve. It should be noted that this t_0 has no biological basis, but positions the von Bertalanffy section of the growth curve in relation to the linear growth phase, so that a relationship between size and absolute age can be describes (Fig. 2.2).

The accuracy of combining the two curves was checked using the tagged abalone released at sizes <80 mm and recaptured >80 mm. Their age at time of release was estimated with the straight line equation and together with their time at liberty used to calculate their age when recaptured. Using the estimated age of recapture an expected size was calculated with the von Bertalanffy equation for comparison with their actual size of recapture. The hypothesis that actual sizes were different to expected sizes was tested with a paired t-test and rejected ($p>0.10$; $t=0.345$; d.f.=37).

2.3.3 Natural Mortality

Using the age-length key described by the analysis of growth, the length–frequency histograms were re-analysed. The age-length key was used to estimate the mean length of the size classes >80 mm and a standard deviation of 6 mm was assumed for these larger distributions, this being the approximate standard deviation estimated for the smaller size classes.

With these values, Mix was used to estimate the proportion of each sample represented by each of the youngest eight age classes. These year classes have been nominated as follows: Mode A mode began recruiting in October 1984, while it is assumed that Mode B began recruiting in October 1983 and Mode C in the previous

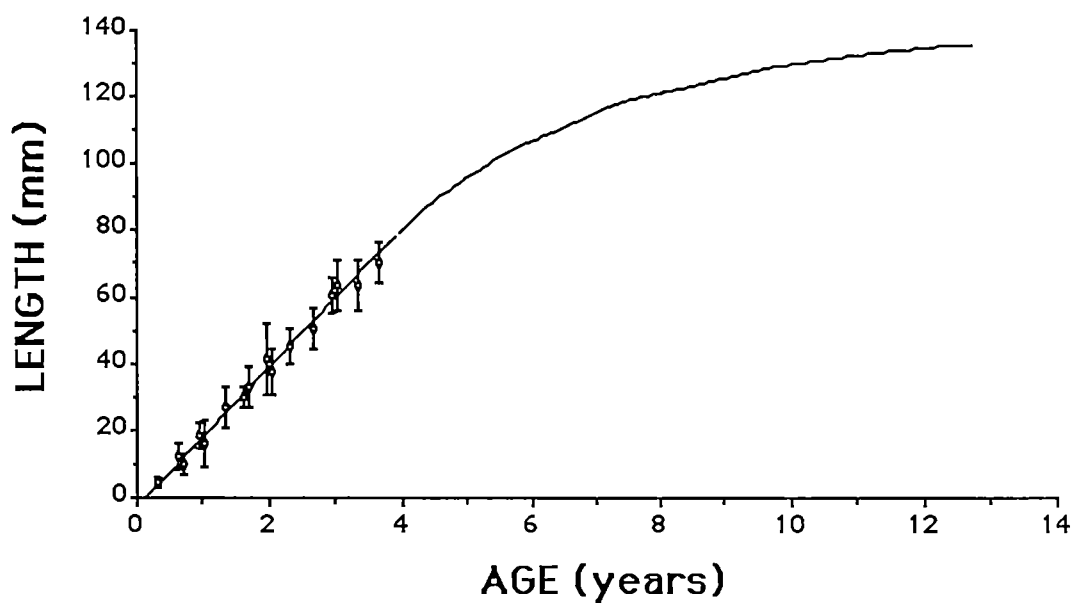


Figure 2.2

Growth curve estimated for *Halargyreus* at the Blubber Head study site. Curve uses length at age data derived from length-frequency histograms in Fig. 2.1 to describe < 80 mm section of the curve, and von Bertalanffy parameters derived from tag-return data to describe the >80 mm section. Error bars for mean length at age regression points: \pm standard deviation of distribution.

year (Fig. 2.1). The largest size class fitted by Mix in the October 1984 sample was Mode G which it is assumed began recruiting in 1978. The error associated with the estimated proportions indicated that the quality of these estimates declined for the size classes >80 mm. This prevented the analysis from being extended beyond the youngest eight year classes.

The estimated proportions were used to calculate the density of each year class in each sample. If the estimated densities of each mode (\log_e -transformed) are regressed against age the instantaneous rate of total mortality can be estimated (Fig. 2.3). The estimated density of Mode A in October 1984 was omitted from this analysis as this year class was clearly not fully recruited at that time. When the individual year classes were analysed separately only the regression for mode B was significant ($r=0.94$, $t=4.71$, $n=5$, $p=0.018$) suggesting an instantaneous mortality rate of 0.698. The lack of significant relationships can be attributed to the small number of points being regressed and the error associated with the initial density estimates.

Despite the limitations of this analysis, it is evident that the density pattern observed does not show the simple log-linear decline that would be expected if a constant mortality rate was responsible for the declining density of successive modes. Crude estimates of the instantaneous mortality rates can be derived for each mode by subtracting the initial and final density measured for each mode (\log_e -transformed) and dividing by the time between measurements. When these estimates are plotted against the mean age of each mode (Fig. 2.4), a significant relationship is revealed between mortality rate and age ($r=0.80$, $t=2.95$, $n=7$, $p=0.032$). This level of significance is increased if the mean size of each mode is used instead of the age ($r=0.83$, $t=3.37$, $n=7$, $p=0.020$).

2.3.4 Breeding

The smallest abalone observed to have free eggs within its gonads had a maximum length of 91 mm and the gonad indices of the abalone increased markedly at a size >85 mm (Fig. 2.5). These two observations suggest that some individuals in the population mature at approximately 90 mm. The fact that the gonad index reaches maximal values at >110 mm indicates that by this size most abalone in the population are mature.

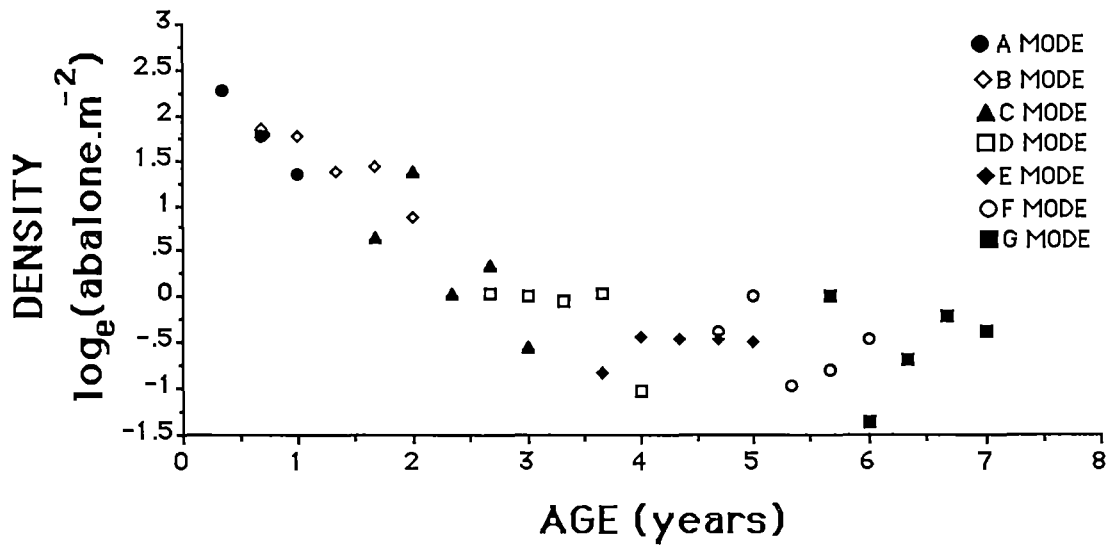


Figure 2.3

Density of Modes A-G (\log_e -transformed) at the Blubber Head study site, plotted against age (y). Density of mode A in October 1984 excluded, since the year class was not then fully recruited.

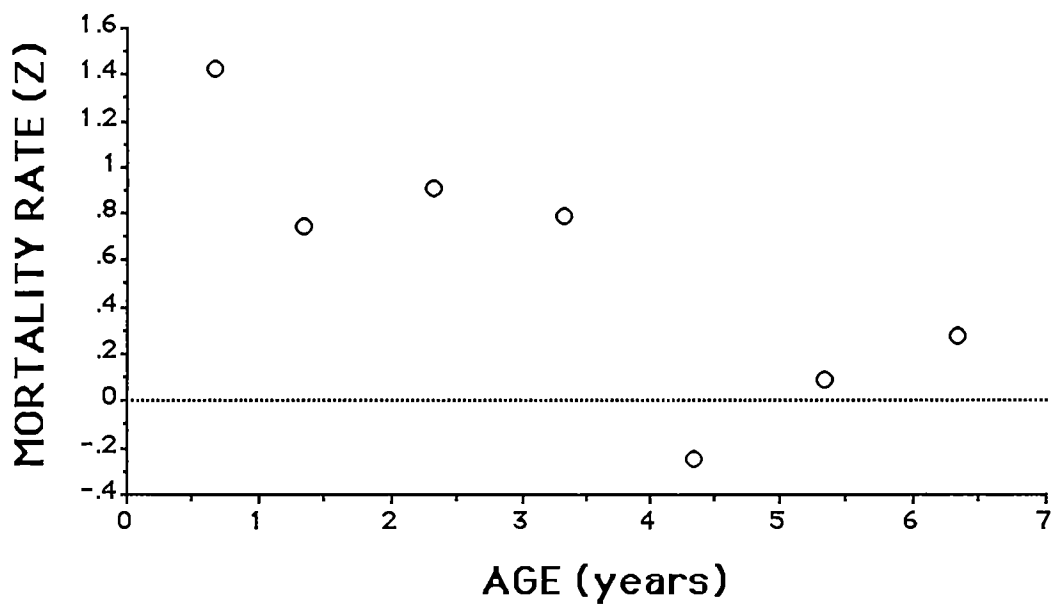


Figure 2.4

Mortality rates, Z , of Modes A-G plotted against the mean age (y) of each mode. Dotted line: $Z=0$.

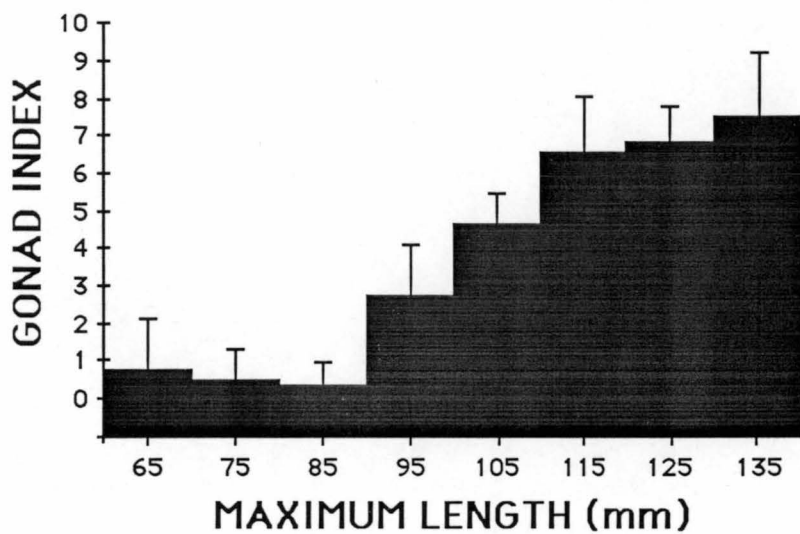


Figure 2.5

Relationship between size and gonad index (proportion of visceral mass cross section made up by gonad x 10) of abalone collected during July 1986; bars indicate 95% confidence intervals, approximately 20 individuals per 10 mm length class.

2.3.5 Emergence

The modal length of abalone collected by divers from the non-cryptic habitat was 110 to 115 mm and 80% of the sample were greater than 90 mm (Fig. 2.6b). These data, when considered with the reproductive data, suggest that primarily mature abalone emerge from the cryptic habitat. The measured density of abalone >90 mm in maximum length prior to the collection of emergent abalone was 0.71 ab.m⁻², and 0.07 ab.m⁻² after the collection. This suggests that almost all mature abalone in this population are non-cryptic.

2.4 DISCUSSION AND CONCLUSIONS

2.4.1 Recruitment to the Population

The length-frequency histograms from February 1984, February 1985, October 1985, and subsequent sampling in 1987 (v. 3.3.2.d) suggest that the protracted period of recruitment during October-February of each year is a relatively stable feature of this population. As the recruitment observed by this study was of 30 to 45 d-old individuals, a spawning season of August-January is suggested. This is consistent with the results of other studies of this species, conducted in this general area (Harrison & Grant 1971, v. 3.4.2).

2.4.2 Growth

The straight line growth observed for the smaller size classes of abalone in this study has been observed or hypothesised for haliotids in a number of other studies (Forster 1967; Newman 1968; Poore 1972b; Koike 1978; Hayashi 1980a; Saito 1981). Several other studies have observed the early growth of haliotids to be non-linear although the departure from linear in these studies has often been slight and in some studies appears to be more assumed than observed (Shepherd & Hearn 1983; Shepherd *et al.* 1985; Clavier & Richard 1986b). A number of authors have also experienced difficulty matching the growth of juvenile and adult abalone using a von Bertalanffy curve (Poore 1972b; Sainsbury 1982a). Poore (1972b) used a von Bertalanffy curve in the same way as it has been used in this study to describe only the upper portion of the growth curve. Yamaguchi (1975) discussed the limitations imposed by using von Bertalanffy curves to describe invertebrate growth more

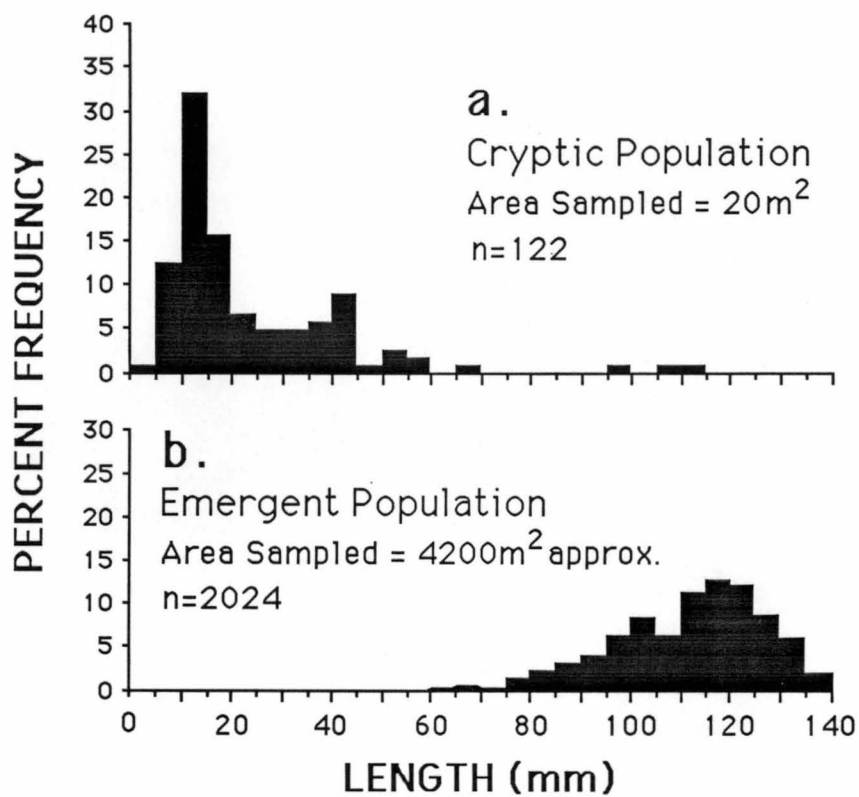


Figure 2.6
Length-frequency histograms of cryptic population of *Haliotis rubra* remaining after removal of emergent individuals (a) and of emergent individuals collected (b); July 1986.

generally, but particular when extrapolating curves, based on tagged adults, to describe juvenile growth. Yamaguchi found that if juvenile growth was not studied independently there was a serious risk of overestimating juvenile growth. A conclusion that is entirely consistent with the findings of this study.

The growth rates found by this study, particularly for the younger age classes, are lower than those documented by Harrison and Grant (1971) or Shepherd and Hearn (1983) who studied *H. rubra* in Tasmania and South Australia respectively. This could be explained by the known intra-specific variability of haliotid growth rates (Leighton & Boolootian 1963; Forster 1967; Harrison & Grant 1971; Shepherd & Laws 1974; Sainsbury 1982a) and the emphasis these studies placed upon tagging data. In most of the earlier studies t_0 was assumed to have a value of approximately zero. If this assumption had been made in the current study and used with the mark-recapture data the age of an abalone at any given length could have been underestimated by up to 17 months.

2.4.3. Mortality

The instantaneous rate of mortality estimated by this study for 1+ abalone is approximately 0.70 annum^{-1} (50% survival. annum^{-1}) but declines with age or size. During this study, the population above a legal minimum size limit of 127 mm was vulnerable to fishing pressure. However all the size classes under study were below this legal minimum size limit, rendering them invulnerable to legal fishing. In addition, the majority of the age classes under study were also living in the sub-boulder population and thus unlikely to be prone to illegal fishing pressure. For these reasons it is unlikely that any form of fishing mortality had affected the observed mortality rates. Consequently, it can be assumed that the mortality rates observed in this study are natural rates of mortality.

Because mortality declines with age, a concave downward or Type III survivorship schedule (Deevey 1947) is apparently applicable for *H. rubra*. This contrasts with the study of Shepherd *et al.* (1982), who found that mortality acted at a constant rate over time and proposed a log-linear or Type II survival curve for abalone. However, the study of Shepherd *et al.* concentrated on the older age classes, which on the basis of our results can be expected to experience relatively low and stable rates of mortality.

There is considerable circumstantial evidence in the literature to suggest that a concave downward survival curve applies generally to abalone populations. Tegner and Butler (1985b) cite several Japanese studies documenting between 21 and 37% survival per annum for juvenile abalone released into the environment during reseeding trials. These rates increased if the size of release was increased. In their own study Tegner and Butler recorded a survival rate of between 8 and 65% for released juvenile hatchery abalone and approximately 12% for natural abalone. These studies are almost exclusively based on hatchery produced abalone released into the natural environment and, because of this, are not strictly comparable with studies of wild populations. However, the consistency of their results with those of the current study is of considerable interest. A low survival rate for juvenile wild populations is also suggested by Hines and Pearse (1982) who postulated that high mortality rates must exist after observing a turnover rate of 92% per annum in a stable abalone population which was heavily predated by sea otters.

In contrast to the poorly detailed survival of juvenile abalone, survival rates of mature haliotids have been well documented (Doi *et al.* 1977; Beinssen & Powell 1979; Sainsbury 1982a; Shepherd *et al.* 1982; Fournier & Breen 1983) as being high (65 to 90% survival.annum⁻¹). Accepting that the mortality rate of abalone declines with age or size reconciles the high survival rates observed in adult haliotid populations with the relatively low juvenile survival rates observed in this study. This form of survivorship has been documented in other studies of molluscan species (e.g. Creese 1981; Vincent *et al.* 1981; Seager 1982; Berg & Alatalo 1985), and perhaps should be expected for abalone if predation is considered likely to be the major cause of natural mortality. That is because smaller abalone with weaker shells and weaker powers of attachment to the substratum are probably more prone to predation.

The technique used to sample abalone in this study increases and standardizes searching efficiency compared to the techniques of visual searching used in most other studies, although it is still unlikely to be sampling the youngest age classes with absolute efficiency (Prince & Ford 1985). However, Powell *et al.* (1984) found that even with a technique that is 100% efficient, the temporal resolution of the sampling regime can cause recruitment density to be underestimated by at least a factor of ten, since the life span of many of the animals recruiting to the population is so short that they live and die between samples and thus are not detected as being

part of the population. Consequently, the estimated rate of natural mortality for *H. rubra* in their first two years of life is undoubtedly an underestimate, and it is likely that an accurate measurement would further accentuate the fact that mortality rates decline with age.

2.4.4 Reproduction and Emergence

Haliotis rubra at Blubber Head begins maturing at approximately 90 mm or at about 4 to 5 y of age. Shepherd and Laws (1974) studied this species in South Australia and observed maturity at 3 to 4 y of age. Harrison and Grant (1971) found that the size of first maturity in a Tasmanian population of *H. rubra* could be as low as 70 mm and that all individuals were mature by 95 mm. From their growth data this would indicate 2 to 4 y as the age of first maturity. However, as discussed (v. 2.4.2) it is probable that the ages of maturity estimated by these earlier studies are based on an overestimation of growth and this may explain the slightly older age of first maturity documented by the present study. The fact that the gonad index for the population does not reach maximal values until >110 mm suggests that many individuals do not mature until 6 to 7 y of age.

The age at first maturity coincides with the end of the linear growth phase. This is as expected as abalone have been observed to transfer energy from somatic growth into egg production at this stage of their life (Peck *et al.* 1987). This age and size also coincided with the movement of abalone from a cryptic to a non-cryptic habitat.

Shepherd (1973) and Witherspoon (1975) noted that *H. rubra* and other species of abalone became less cryptic with increasing size, although they did not attempt to correlate this with any biological change. Shepherd hypothesized that juvenile abalone remain cryptic to avoid predators, leaving the cryptic habitat when they reach a size that is less prone to predation. These data offer the interesting suggestion that the onset of maturity is also associated with this change in micro-habitat. The data presented here are not sufficient to argue conclusively that this is the sole, or even one, of several possible factors affecting the emergence of *H. rubra* from cryptic habitats. However, aggregation (Shepherd 1986b) and movement of abalone to local elevations (Breen & Adkins 1980) during the breeding season have been documented for other species of abalone. If *H. rubra* exhibits these behaviour patterns they could provide the mechanism linking

emergence with the onset of sexually maturity in this species.

2.4.5 Population Structure

The size structure of the abalone population, evident in the length-frequency histogram, remained relatively stable over the time span of this study. The smallest length intervals (0–50 mm) were the most numerically abundant, the middle length intervals (50–90 mm) least abundant, and the largest size intervals (>90 mm) moderately abundant. This structure is apparently maintained by the effects of growth and mortality. The juvenile year classes (<90 mm) grow rapidly and remain relatively distinct in the length frequency histograms so that the effect of high mortality rates can be clearly observed in the declining numerical abundance of abalone in the 0 - 90 mm length intervals. Growth and mortality rates decline in the mature year classes (>90 mm) so that the modes of older year classes coalesce. This causes the apparently anomalous situation where abalone in length intervals >90 mm are numerically more abundant than those in the 5–90 mm length intervals.

In several other studies, the low numerical abundance of the mid-sized length intervals compared to that of the largest size intervals, has been observed and used to infer recruitment failure (Forster *et al.* 1982; Sainsbury 1982b). However, from the present study it would appear possible that those results may have been based on an artifact of length-frequency histograms which would not have been apparent had it been possible to accurately age the abalone. It seems possible that undetected size- or age-dependent mortality within those populations, rather than recruitment failure, may have been the cause of the population structure observed by those studies.

Most studies of abalone have not observed significant numbers of juveniles and have concluded that abalone populations are dominated by accumulations of mature abalone. This has led to the assumption that abalone populations are relatively static and non-productive (Tegner *in press*). This does not satisfactorily describe the abalone population I observed during this phase of this study. I observed that juveniles were abundant, and that the juvenile phase was characterized by a dynamic population structure with high levels of recruitment, growth and mortality. The adult phase of the population conformed to the observations made in other studies, being stable and relatively static; significantly this part of the population is more

easily collected than the cryptic juvenile population.

2.5 CONCLUSIONS

The results of this study indicate that populations of *H. rubra* occupy two distinct micro-habitats. Juveniles are entirely cryptic, living within the rocky substratum they inhabit, while adults live on the surface of the substratum. The growth of juveniles is approximately linear and unlike the growth of adults, cannot be described with von Bertalanffy parameters. The juvenile population is abundant, but experiences high levels of mortality. Mortality declines with age and/or size.

CHAPTER 3

LARVAL DISPERSAL AND THE RELATIONSHIP BETWEEN THE ABUNDANCE OF STOCK AND RECRUITMENT IN *HALIOTIS RUBRA*.

3.1 INTRODUCTION

The ability of larvae to disperse is an important determinant of the scale of a unit stock in any marine species (Hancock 1979) in that it directly affects the potential of species to re-colonize areas from which they have been removed (Mileikovsky, 1971). However, to be relevant to fishery scientists, information about the ability of larvae to disperse must be more than mere documentation of the maximum possible distance over which larvae may travel. While this type of information may be of relevance to bio-geographers and others interested in recruitment and colonization processes which occur on a geological time span, fishery managers are interested in a time scale similar to that of the human life. A fishery based study of larval dispersal must orientate towards recruitment and dispersal events which will determine the dynamics of a fishery. For this reason the question becomes: not, 'How far can larvae travel?', but, 'Where will most of the recruitment occur?'

In this chapter when I use the word 'recruitment' I mean the process by which new individuals are added to the general population through the processes of settlement and metamorphosis, as opposed to the transition from the unexploited to exploited parts of the population.

Prior to this study, no studies on the dispersal ability of haliotid larvae had been published. The paucity of work in this area is due mainly to the difficulty of finding haliotid larvae and juveniles within their natural environment (Tomita *et al.* 1977; Breen & Adkins 1980). From observations made under laboratory conditions it has generally been assumed that the lecithotrophic haliotid larvae are pelagic and disperse widely (Mottett 1978; Fedorenko & Sprout 1982; Sluczanowski 1984; Tegner & Butler 1985a).

The development of the anaesthetic technique for sampling haliotid populations (Prince & Ford 1985) made it possible to obtain samples of large numbers of haliotids within months of their settlement and allowed patterns of recruitment to the population to be observed directly. During the initial sampling at Blubber Head (v. Chapter 2) the qualitative observation was made that the size composition of the abalone population was extremely variable over small distances (20-40 m). One explanation for this observation could be that larval dispersal is more restricted than has been assumed in the literature and this possible explanation suggested an interesting and previously unplanned avenue of research.

Pelagic larvae are apparently the most widespread form of larvae amongst benthic marine invertebrates (Thorson 1950; Mileikovsky 1971); however, free swimming non-pelagic larvae (dermersal development larvae) have been found in a range of marine organisms (e.g. Millar & Hollis 1963; Pearse 1969; Gerrodette 1981; Olson 1985; Knowlton & Keller 1986), including gastropods (e.g. Shuto 1983).

Knowlton and Keller (1986) demonstrated that the recruitment of a tropical alpheid shrimp was at least, partially localized despite the fact that the larvae are free swimming for at least 7 days. They suggested that the assumption of dispersed recruitment for marine invertebrates with free swimming larvae has, in fact, been made too readily in studies of these animals.

The objective of this section of the present study was to test the extent of larval dispersal in natural populations of haliotids. A number of studies have tested this premise for a range of other marine organisms by experimentally removing and/or introducing reproductive stock and observing subsequent settlement or recruitment patterns (Anderson & North 1966; Dayton 1973; Sebens 1983; Dayton *et al.* 1984; Olson 1985; Knowlton & Keller 1986; Vandermeulen & DeWreede 1986).

No techniques exist for directly measuring abalone settlement. However Connell (1985) presented evidence to suggest that, except at very high densities, invertebrate recruitment patterns were likely to accurately reflect settlement patterns. This principle, and the possibility of directly measuring haliotid recruitment using the anaesthetic technique, suggested the possibility of experimentally manipulating breeding stock to test the dispersal ability of haliotid larvae. Basically, the design of the experiments described here involved reducing the density of breeding stock along a section of shoreline and measuring the subsequent juvenile recruitment.

The hypothesis being tested by this experiment is that the abundance of abalone recruitment is related to the immediate density of adult abalone. The logic is that if abalone larval dispersal is relatively large, then abalone recruitment will not necessarily depend on the immediate density of breeding stock. However, if larval movement is restricted, then the occurrence of abalone recruitment will be determined by the presence of breeding abalone in the immediate area.

This experimental study was conducted in two parts. The first phase was a simple preliminary experiment which was conducted over the September - November 1985 breeding season in order to test the original qualitative observations. The original

experimental design was then refined in the light of the first experiment and a second confirmatory experiment was conducted over the 1986 breeding season.

3.2 PRELIMINARY EXPERIMENT

3.2.1 Material and Methods

3.2.1.a Study Area

The study area at Ninepin Point, Tasmania (43°17'S, 147°10'E.) is a uniform section of rocky coastline extending 70 m from high water mark to a depth of 6–9 m. The bottom is composed of three layers of boulders resting on silt. The boulders are of irregular shape and mostly 30–40 cm greater diameter by 10–20 cm lesser diameter. The macroalgal community of the area has three strata; the upper stratum (>1 m) consists of *Macrocystis pyrifera* (L.) C. Agardh, the middle stratum (0.15–1.0 m) is dominated by the species *Acrocarpia paniculata* (Turn.) Aresch., *Cystophora moniliformis* (Esper), Wom. & Niz. and *Sargassum verruculosum* (Mertens) C. Agardh, The lowest stratum (0–0.15 m) is dominated by encrusting corallines. On the exposed surface of the boulders these corallines are overgrown by filamentous algae including *Cladophora* sp., *Ceramium* sp., *Polysiphonia* sp. and *Calithamnion* sp., and small fleshy algae of the genera *Zonaria*. In depths >6 m algae of the genera *Peyssonnelia*, *Thamnoclonium* and *Caulerpa* commonly overgrow the crustose corallines which are abundant at these depths.

In this area *M. pyrifera* is of limited importance, being confined to a narrow (5–10 m in width), diffuse and irregular band about 20 m from the shoreline in depths of 2–3 m. As a consequence, despite the presence of *M. pyrifera*, in depths <4 m the algal community is typical of a furoid association indicative of slight to moderate wave action (Sanderson & Thomas 1987). This is in contrast to depths >4 m where the characteristics of the algal community change, and only the lowest strata is found.

This entire section of shoreline has carried a natural population of *H. rubra* at sufficient densities to support continuing amateur and professional fishing over the previous 15 y, suggesting regular recruitment of abalone.

3.2.1.b *Breeding Stock Removal*

The existence of recent recruitment and the size of the smallest abalone present before the experiment was established on 3 August 1985 using the anaesthetic technique (detailed below). Following this, the central 90 m section of shoreline was marked out for the removal of abalone breeding stock. To aid in the allocation of diving effort during the removal process, this area was divided into three segments, sites 4, 5 and 6 respectively (Fig. 3.1), each about 30 m long. These were delineated with chain laid on the seabed perpendicular to the shore from low water mark to the edge of the sandy substrate.

On five occasions between 10 August 1985 and 18 September 1985 all abalone found of >60 mm maximum shell length were removed from each of the three sections by divers. Disturbance of the substrate during collection was minimal as abalone were only taken from the exposed boulder surfaces and no boulders were moved during the searches. It was recognised that a proportion of the >60 mm abalone would not be detected by these searches, but minimal disturbance of the substrate was considered more important than maximal reduction of the population. The maximum length of each abalone captured was measured to the nearest millimeter. The number removed from each of the three 30 m segments and the total diver hours expended in each area was recorded for each of the first four searches. The fifth and final search was of a shorter duration (total diver hours = 4.5) and on this occasion the catch and effort was not separated by area.

3.2.1.c *Breeding Studies*

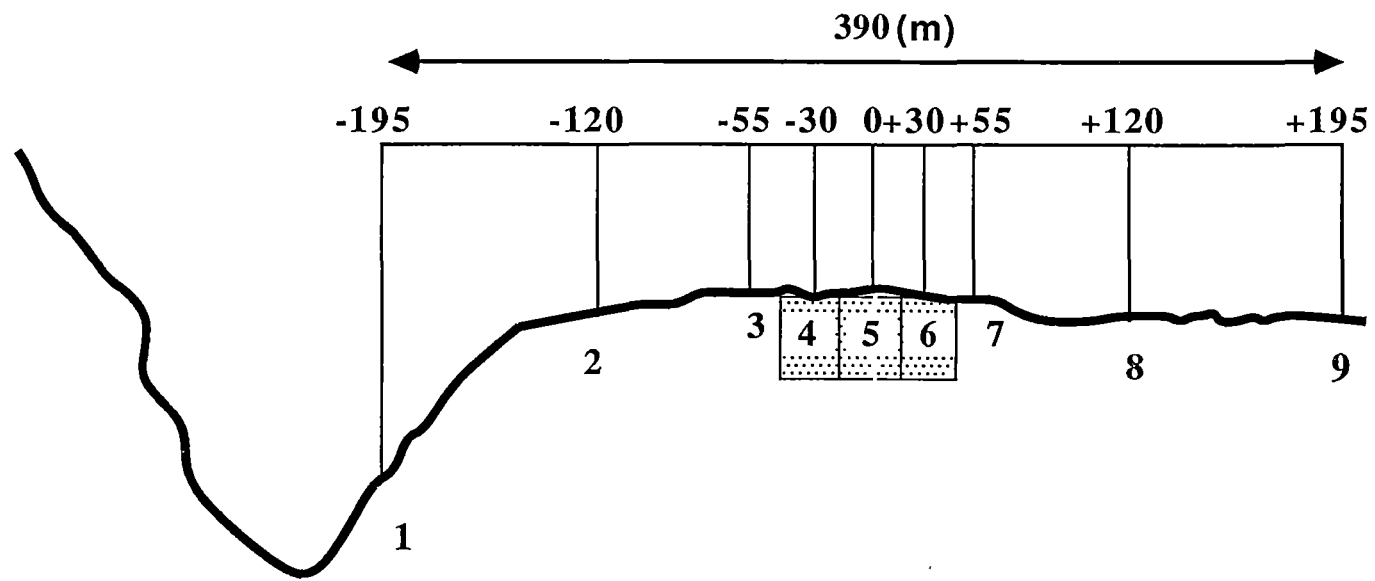
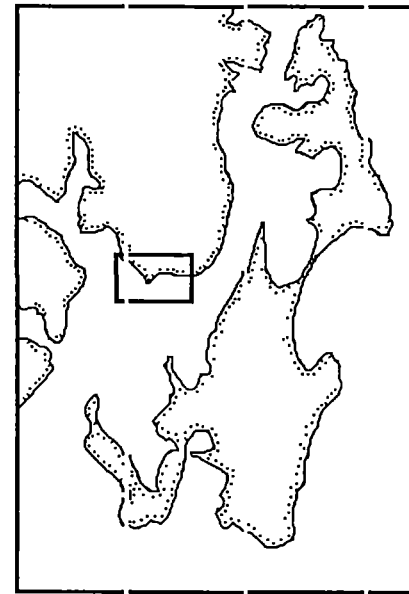
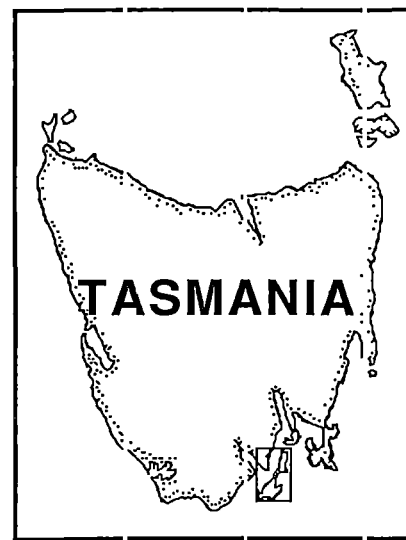
From the initial removal (10 August 1985), sub-samples of 20 abalone from each 10 mm size class were retained for gonad index studies using the methods described in Section 2.2.6.

A further sample of 83 abalone, covering the size range indicated by the gonad index study to be mature, were collected between the 10-16 September 1985 for an analysis of fecundity. The fecundity of abalone at the study site was also measured after the removal of breeding stock to determine the timing of spawning at the site.

The method used to estimate fecundity was based on that of Sainsbury (1982a). After fixation in 10% formalin the gonad was dissected from the hepatic gland and gently teased apart into 50-250 ml of water. The water was agitated until all the eggs

Figure 3.1

The location and layout of the study site at Ninepin Point, Tasmania, used in the preliminary experiment. The shaded area indicates the area from which abalone were removed and the numbers indicate sampling sites. Distances (m) are given from the centre of the removal area.



were free and evenly dispersed, two or three 0.5-1.0 ml samples were then taken. Each sample was placed in to a counting chamber marked with a grid. In the counting chamber the yolked eggs in five standard squares were counted. Total fecundity was calculated by multiplying out the the various sub-sampling factors.

3.2.1.d *Post-Removal Sampling*

In February-March 1986 the abalone populations at nine sites were sampled. The sites (Fig. 3.1) covered 390 m of shoreline, and were centred on the segment of shoreline from which the breeding stock was removed 0 m, (site 5) and 30 (4 & 6), 55 (sites 3 & 7), 120 (sites 2 & 8) and 195 m (sites 1 & 9) either side of the centre. This spacing was selected so as to maximize the probability of observing any effect caused by removing the breeding stock.

The anaesthetic technique (v. 2.2.2) was used to sample the abalone at these sites. Twenty areas of 1 m² at each site were selected by throwing a quadrat from an anchored vessel. Stratification was achieved between sites by anchoring the vessel 10 m off shore while selecting the initial 10 squares at each site, and 35 m off shore while selecting the remaining squares. All abalone collected were measured for maximum shell length, to the nearest 1 mm.

The length frequency data from the samples were analysed using the Macdonald and Pitcher mixture analysis 'Mix' (Macdonald & Pitcher 1979; Macdonald & Green 1985). The cut off points between the different size distributions of abalone described by this analysis were taken as the points where two consecutive distributions overlapped. These points were calculated using the formula:

$$X = ((x_2 + x_1) \times 0.5) + ((s_1^2 \times s_2^2) \times \log_e(p_1 / p_2)) / (x_2 - x_1)$$

where X is the cutoff point (mm) and x_i , s_i^2 and p_i are the estimated means, standard errors and proportions of the i-th distribution respectively.

The densities of abalone detected showed a tendency to be positively skewed about the mean. A log(X+1) transformation was used to normalize the data. The differences in densities between areas was tested with a two-tailed Student's t-test using a significance level of 0.05. This method was also used to test the significance of correlations between adult and juvenile densities.

3.2.2 RESULTS

3.2.2.a *Breeding Studies*

Analysis of the gonad index of the abalone collected from the research site on 10 August 1985 showed that for the size classes examined (>60 mm) the index increases with size up to the length of 100 mm; a sharp increase was observed between 90 and 100 mm. Maximal values were found in abalone of 100-145 mm maximum length. The relationship between fecundity and maximum shell length for animals collected 10-16 September 1985 was best described by a single variable regression:

$$F = (0.028 \times ML) - 2.415$$

where F is fecundity measured in millions of eggs and ML is maximum shell length in millimeters. This relationship was found to be highly significant ($r=0.62$; $n=83$; $p<0.001$). This line intersects the x-axis at 87 mm, suggesting this is approximately the size of first maturity, which is in relatively close agreement with the results obtained by examining the gonad index. These results indicate that the onset of sexual maturity in this area probably occurs when the abalone attain the length of 87 mm and that by the length of 100 mm virtually all the abalone are sexually mature.

A sample of 45 mature female abalone were collected on 27 September 1985. Over 50% of the gonads showed signs of extensive spawning, 26% had fecundities <5% that predicted by the above relationship. For this sample the relationship between maximum length and fecundity was not found to be significant ($r=0.23$; $n=45$; $p>0.1$). This indicates that a widespread spawning had occurred in the study area between 18-27 September 1985. This timing is consistent with the observations Harrison and Grant (1971) made for Tasmanian populations of *H. rubra* and suggests that a general spawning occurred within 9 days of the final search for breeding stock. The water temperature at the study site at this time was approximately 13°C.

3.2.2.b *Breeding Stock Removal*

Between 10 August 1985 and 18 September 1985 divers spent 85.8 diver hours searching for abalone. A total of 3 584 abalone were removed from the 90 m section of shoreline encompassing sites 4-6, of which 3 274 (91%) were >87 mm

(Fig. 3.2). Over the entire area catch rates fell from 104.0 >87 mm ab.h⁻¹ during the initial search to 9.8 >87 mm ab.h⁻¹ during the final search (Fig. 3.3). Using the number of abalone caught in each area and the size of the areas (1 793, 1 987 and 1 674 m² for areas 4, 5 and 6 respectively), the searches can be calculated to have reduced the density of mature abalone by 0.54, 0.51 and 0.77 ab.m⁻² in each area respectively.

Accepting the catch rates as an index of relative abundance the estimated decrease in mature abalone abundance in each area between the first and fourth visit is 89.7, 92.0 and 87.3%. From these data it can be estimated that the density of mature abalone within each area before the searches was approximately 0.60, 0.55 and 0.88 ab.m⁻² respectively. It can also be estimated that after the searches the remaining density of mature abalone in each area was 0.06, 0.04 and 0.11 ab.m⁻². In making these estimates only the catch rate data from the first four searches have been used, as data were not separated by individual area, during the short (4.5 diver h) final search. The final catch (44 ab. >87 mm) has been proportioned equally between the areas. Any bias caused by this process is likely to be negligible due to the small number of abalone removed by the final search.

The movement of adult *H. rubra* at the Blubber Head, which is a similar habitat to the Ninepin Pt. site, has been observed to be very limited, 10–20 m.annum⁻¹ and without along shore directionality (White & Whyte, pers. comm.). Therefore because widespread spawning commenced within 9 days of the final search, it can be assumed that the estimated densities of mature abalone after the searches approximate the density that was present in each area during spawning.

3.2.2.c Post-removal Sampling

Figure 3.4a shows the density of mature (>87 mm) abalone measured at each site in February-March 1986, four months after spawning had occurred. Sites 1-3 had a generally low level of mature abalone when compared to sites 7-9. The effect of removing breeding stock from sites 4-6 (sites 4-6 pooled) was still clearly evident at the time of sampling, with the density of mature abalone being significantly lower ($t=4.15$; $P<0.001$) than the mean density at the other sites (sites 1-3, 7-9 pooled). The effect of migration back into the area over the period since the removal is indicated by the shape of the depression in densities, with the highest value (site 6)

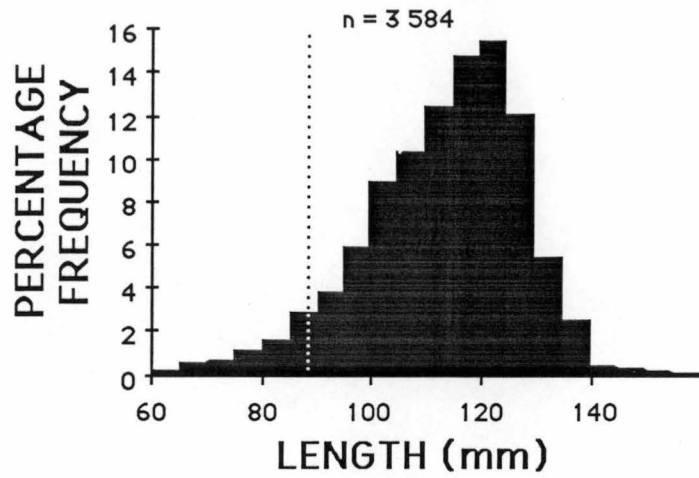


Figure 3.2
Length-frequency histograms for *Haliotis rubra* collected during searches of the removal area. The dotted line indicates the size of first maturity (87 mm).

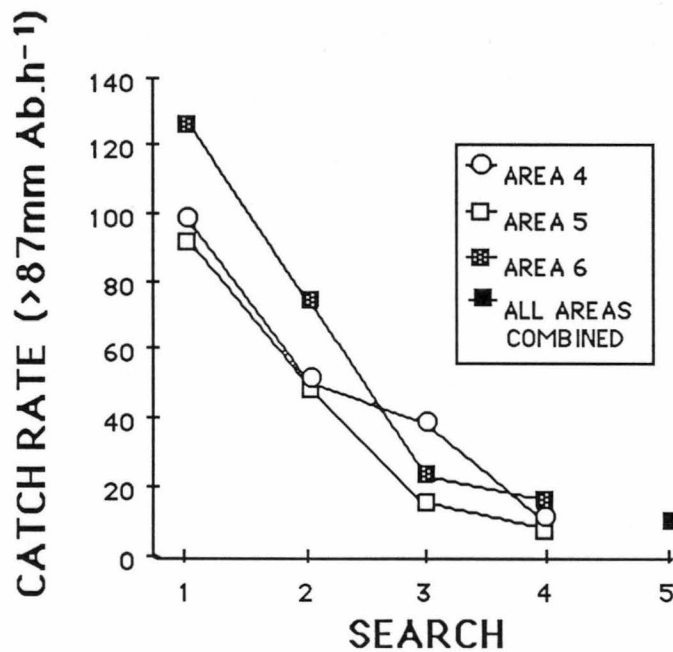


Figure 3.3
Catch rates of *Haliotis rubra*, in each section of the removal area, during each period of searching. N.B. The data was not separated by area for the fifth search.

Figure 3.4

The density of *Haliotis rubra* measured at each sampling site in February - March 1986, using the anaesthetic technique (solid line): A, >87 mm abalone, broken line indicates estimated density before searches, dotted line indicates estimated density during spawning; B, 0+ mode; C, mode B; D, mode C; E, mode D; F, mode E. Bars indicate $\pm 95\%$ confidence interval, shading indicates sites from which mature abalone were removed.

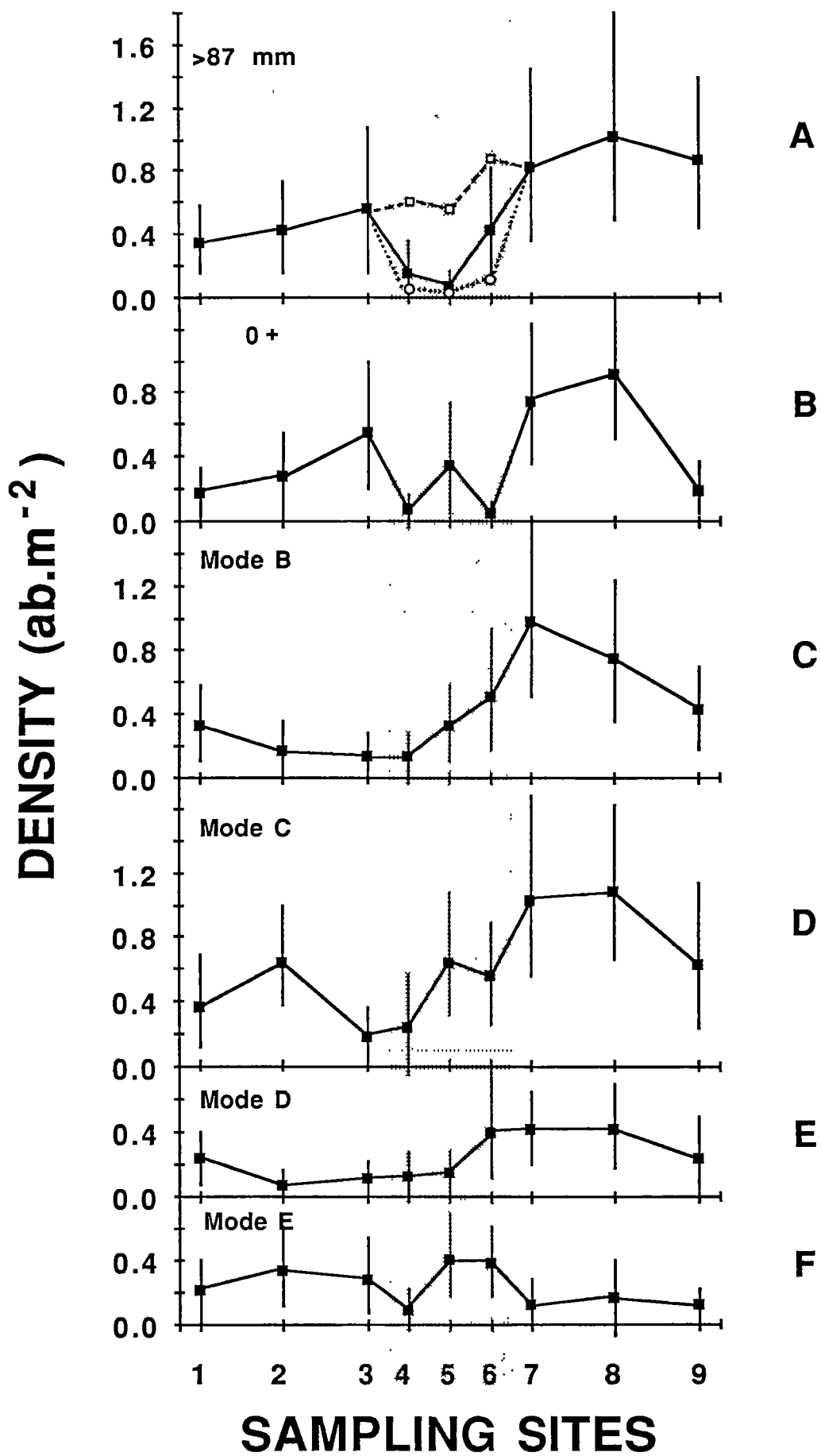


Figure 3.4

being adjacent to the highest adjoining outside value (site 7) and the lowest value being at site 5, furthest from the source of immigrating abalone.

Figure 3.5 shows the length frequency histograms for all 0-60 mm abalone collected during anaesthetic sampling in 1 mm size classes. The figure shows the results of preliminary sampling conducted in August 1985 and the sampling conducted in February and March 1986. This latter data are shown grouped for sites 1-3, 4-6, 7-9 and for all sites pooled.

When the Macdonald and Green (1985) Mix program was used to describe the 0-42 mm length-frequency data the best fit was achieved with 10 log-normal size distributions, with means at 3.3, 8.4, 12.3, 15.1, 19.7, 23.7, 27.7, 33.2, 36.4 and 40.0 mm ($\chi^2=7.54$; d.f.=13; $p=0.87$). Because the smallest abalone collected during the preliminary samples in August 1985 was 5 mm in length the smallest size group observed in February and March ($\mu=3.3$ mm) had clearly settled after the removal of breeding stock. The estimated cut-off point between the first and second distribution is 6 mm.

The next best description of the 7-42 mm data grouped the 2nd-4th, 5th-7th and 8th-10th of the former distributions respectively and described these data as 3 distributions. In this latter analysis the estimates converged with the estimated means of each distribution being 14.4, 25.0 and 36.1 mm ($\chi^2=37.1$; d.f.=30; $p=0.174$). To increase the numerical abundance of each size class this grouping of the smaller distributions has been used. However the cut off points between the three larger distributions (17 & 31 mm) have been calculated using the estimated parameters of the smaller component distributions. The size group 43-60 mm is clearly distinct from the smaller size groups and has been treated as a separate size class.

This analysis of the length-frequency histogram is not meant to imply an age for any size group besides the 0-6 mm class. This smallest class was clearly not present in the August 1985 samples, but settled after the searches; consequently, it can be concluded that they represent at least some portion of the 0+ age class. No ages are be attached to the other size classes. However, if growth rates are assumed to be relatively uniform within the study area, it can be assumed that each size class represents some unknown grouping of ages. If this is accepted, and mortality is also assumed to be relatively uniform over the research area, each size group can be

Figure 3.5

Length-frequency histogram for all 0-60 mm *Haliotis rubra* sampled with the anaesthetic technique during August, 1985 and February-March, 1986, the latter samples are grouped for sites 1-3, 4-6, 7-9, and all sites combined.

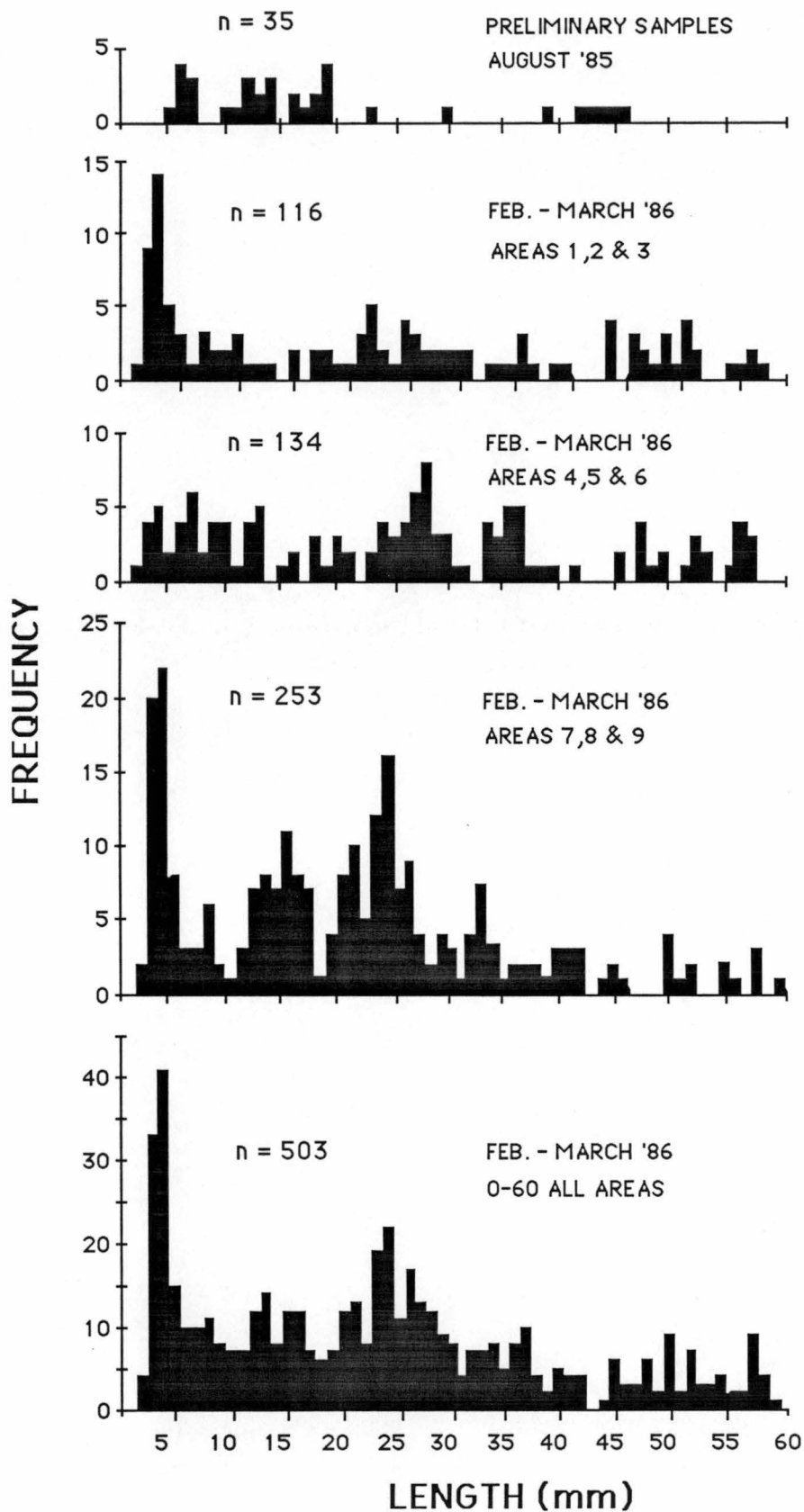


Figure 3.5

used to indicate the recruitment pattern which occurred over some period of the past. For this analysis, the 0-6 mm size group will be referred to as the 0+ and the size groups 7-17, 18-31, 32-42 and 43-60 mm will be referred to as modes B, C, D and E respectively.

Figure 3.4b shows the measured density of the 0+ mode across the sampled sites. The mean density for sites 4-6 (sites 4-6 pooled) was significantly lower than the mean of the other sites (sites 1-3, 7-9 pooled; $t=3.52$; $p<0.001$). The density for the 0+ size group at sites 1-3 was also generally lower than at sites 7-9. These results show that a reduced level of recruitment occurred at sites 4-6 following the removal of mature abalone. This effect was extremely localized, with the reduction in recruitment only being evident within the removal area. This pattern reflects the density pattern of adult abalone at the time of spawning.

In contrast to the observed 0+ densities, the density pattern observed for each of the other modes were generally similar to the pattern of mature abalone, estimated to have existed prior to the removal process. With the exception of mode E all had higher values at sites 7-9 and their density declined relatively smoothly towards sites 1-3 (Fig. 3.4c-f). The density of mode E, showed no obvious trends across the sites. For each of these size classes no significant difference was found between the mean densities at sites 4-6 (sites 4-6 pooled) and the mean density of the sites outside (sites 1-3, 7-9 pooled) the removal area (mode B; $t=1.18$; $p>0.1$, mode C; $t=1.22$; $p>0.1$, mode D; $t=0.287$; $p>0.1$, mode E; $t=1.13$; $p>0.1$). These data indicate that no historical precedence exists for the recruitment pattern observed following the removal of breeding stock.

Linear regressions of the density of these smaller size classes at each site against the density of mature abalone at each site, both before the searches and at the time of spawning, have been estimated (Table 3.1). In this analysis, the estimates of the initial density of mature abalone at sites 4-6 before the searches (0.60, 0.55 and 0.88 ab.m^{-2} respectively) have been used along with the estimated densities during spawning (0.06, 0.04 and 0.11 ab.m^{-2} respectively). The density of mature abalone estimated by the post removal sampling at sites 1-3 and 7-9 have been used as the density at these sites both before the searches and at the time of spawning.

With the exception of mode E, all the modes showed a positive correlation with the density of mature abalone both before and after the removal process. The

density of mode E was not significantly correlated with the density of mature abalone before the searches ($r=0.30$; $n=9$; $p>0.1$) or at the time of spawning ($r=0.54$; $n=9$; $p>0.1$). The relationships between the density of mature abalone before the searches and the densities of modes B ($r=0.70$; $n=9$; $p<0.05$) and D ($r=0.78$; $n=9$; $p<0.05$) at each site are significant, while the correlation with mode C is high but not significant at this level ($r=0.63$; $n=9$; $p=0.064$). The density of 0+ at each site was not significantly correlated with the density of mature abalone before the searches ($r=0.42$; $n=9$; $p>0.1$).

In direct contrast to the above, the density of mature abalone at each site during spawning was significantly correlated only with the density of the 0+ ($r=0.73$; $n=9$; $p<0.05$). These results indicate that the density pattern observed for the 0+ was most closely related to the densities of mature abalone that existed at the time of spawning. While the density patterns of modes B, C and D were most closely related to densities of mature abalone that existed before the removal process.

Table 3.1 Estimated correlations between the density of the 0+ size group, modes B, C, D, and E, and the estimated density of mature (>87 mm) abalone before and after the searches.

Regression variable X-density of >87 mm abalone				
Regression variable Y	Regression equation	Correlation coefficient (r)	t-statistic (n=9)	2-tailed significance
Before Removal				
0+	$y = -0.01+0.55x$	0.42	1.22	0.256
Mode B	$y = -0.17+0.87x$	0.70	2.59	0.032
Mode C	$y = 0.03+0.84x$	0.63	2.15	0.064
Mode D	$y = -0.07+0.47x$	0.78	3.29	0.011
Mode E	$y = 0.34+0.55x$	0.30	0.83	0.430
After Removal				
0+	$y = 0.08+0.60x$	0.73	2.83	0.022
Mode B	$y = 0.20+0.46x$	0.58	1.88	0.096
Mode C	$y = 0.36+0.51x$	0.61	2.04	0.076
Mode D	$y = 0.16+0.17x$	0.45	1.33	0.219
Mode E	$y = 0.32-0.18x$	0.54	1.70	0.128

3.2.3 Discussion

The results of this experiment indicate that for *H. rubra* the density of recruitment is related to the immediate density of spawning abalone. The density of recruitment (the 0+ mode) was significantly lower inside the area from which spawning stock were removed, than outside the area, a pattern which was not evident in the size groups of abalone spawned before this experiment was conducted. In addition, the density of recruitment both inside and outside the area was significantly correlated with the density of breeding stock at each site. Abalone populations have been observed to be stable over time (Hines & Pearse 1982). Thus, the density pattern of the spawning stock before the searches was probably similar to those that existed when modes B, C, D and E were recruited. The density pattern of three of these size classes were more strongly correlated with this previous pattern of breeding stock than with the pattern created by the searches. This is consistent with the finding that, for *H. rubra*, recruitment is directly related to the immediate density of spawning abalone. The fact that the density of the fourth and oldest size class was not correlated with either density pattern of spawning stock may indicate either that some change has occurred in the adult population over time, or that there is some level of mobility amongst juvenile abalone.

In the light of these results, a confirmatory experiment was designed so as to cover some of the weaknesses of the preliminary study. The main modification was the inclusion of replicate sites. To this end four sites were selected for the second experiment, but the scale of the experimental manipulation at each site was diminished.

3.3 CONFIRMATORY EXPERIMENT

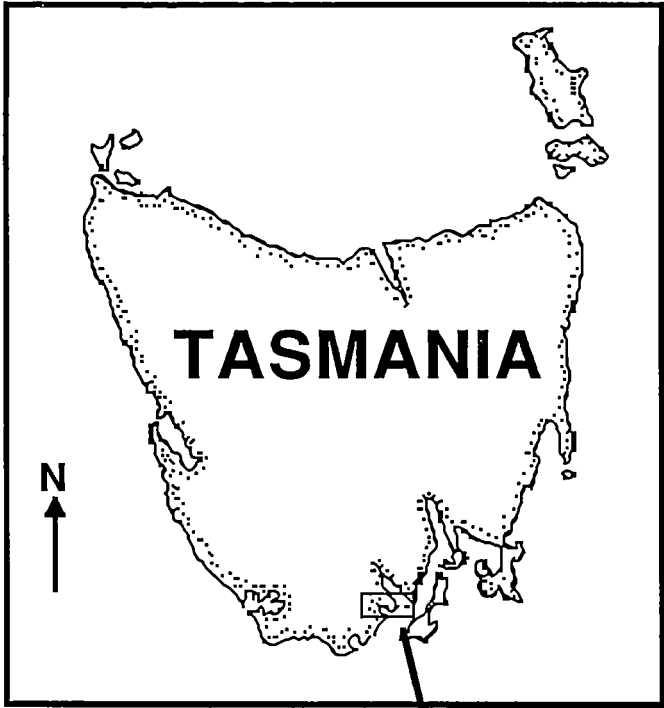
3.3.1 Materials and Methods

Four sites in the southern end of D'Entrecasteaux Channel in Tasmania, southern Australia (43°19'S., 147°04'E.) were selected: Ninepin Point, East Hope Is., North Hope Is. and Blubber Head (Fig. 3.6). The abalone-bearing habitat at each site was similar, with boulders extending from above the high water mark down to approximately 10 m below the low water mark where it ran into sandy substratum.

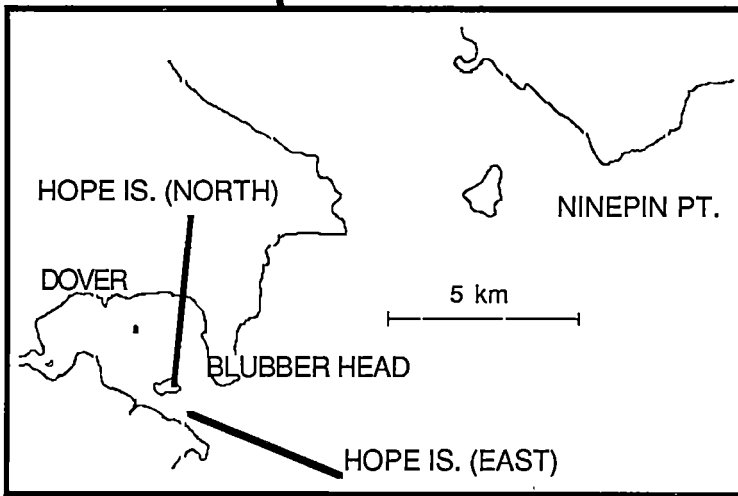
At each site a 180 m stretch of abalone-bearing coastal reef was selected. The

Figure 3.6

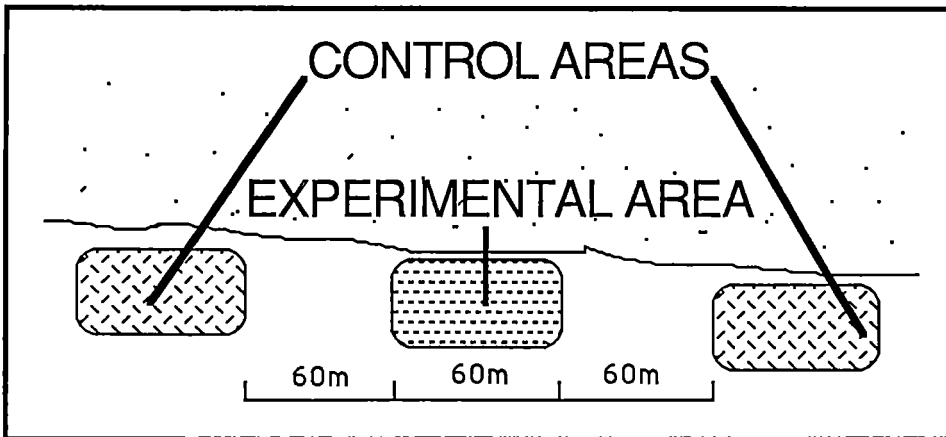
A map of the of D'Entrecasteaux Channel in Tasmania, southern Australia showing the location of the study sites used in the confirmatory experiments (A & B) and the design of these experiments (C).



A



B



C

Figure 3.6

central 60 m section at each site was marked out as an experimental area from which adult abalone were removed. The shoreline at either end of the 180 m section of coastline served as control areas and the breeding stock in those areas was not disturbed (Fig. 3.6). Immediately prior to the removal of breeding stock from each experimental area, the original density of adult abalone within the experimental areas was measured. Because adult *H. rubra* live in non-cryptic habitats (v. 2.4.4) and can be found relatively efficiently by searching divers these density estimates were obtained by divers searching the substrate for abalone in 20 x 1 m² quadrats. The sampled areas were selected by throwing a quadrat from an anchored boat.

Breeding stock removals were conducted during July and August, 1986. During this procedure a team of four divers searched each 60 m segment of shoreline on four occasions. During the searches all abalone > 60 mm (maximum shell length) that could be collected without disturbing the substrate were gathered by the divers. For the sites where reproductive studies had not been completed samples, of abalone were taken so as to determine the size of first maturity.

The density of adult abalone remaining in each experimental area was measured after the searches had been completed. This was achieved by sampling a further 20 quadrats of 1 m² in each area. On this occasion the substratum in 10 of the quadrats was sampled by diver searching and the remaining 10 quadrats were sampled with the anaesthetic technique of Prince and Ford (1985). This latter technique samples abalone >70 mm with the same efficiency as visual searching; however it samples the smaller size classes more efficiently (Prince & Ford 1985). This technique was used to adequately sample the immature size classes so that the size of the smallest size class present could be determined. It was not used throughout the study because it consumes more diving time than visual searching and disturbs the substrate.

Between February and April, 1987 after spawning and recruitment had occurred the abalone populations at each site were sampled a third time. During this post-recruitment sampling the experimental area and the two control areas were sampled at each of the 4 sites. A total of 20 x 1 m² quadrats were sampled in each area using the anaesthetic technique of Prince and Ford (1985).

The movement of *H. rubra* is known to be relatively limited in these types of environments (v. 3.2.2.b) and mortality rates have also been observed to be

relatively low in the adult population (v. 2.3.3). For these reasons it can be assumed that the density of adult abalone measured at the control areas during the post-recruitment sampling approximated the density present at these sites during the breeding period. Because of this, and the logistics of conducting this experiment, the actual density of breeding stock in the control areas was only measured as a part of the post-recruitment sampling. It was assumed that in these undisturbed control areas this density approximated the density that was present during the time of spawning.

As the measured densities of abalone were extremely low, (in many quadrats there were no abalone) pairs of quadrats were randomly selected from within each set of samples and pooled. The measured densities of abalone showed a tendency to be positively skewed about the mean so a $\log(X+1)$ transformation was used to normalize the data.

A simple analysis of variance was used to compare the densities of breeding stock within experimental areas before and after the removal of breeding stock. Nested analysis of variances were used to test between and within site variability of breeding stock and recruitment density. Where variables were used more than once, violating the assumption of independent variables, the Bonferri method was used to adjust the level of significance being tested (Day & Quinn in prep.). Planned comparisons were used to test differences within individual sites (Winer 1971).

Analyses of variance were used to test the significance of different relationships between the density of breeding stock and recruitment.

3.3.2 Results and Discussion

3.3.2.a Breeding Studies

The relationships between fecundity and maximum length at each site were adequately described by the following linear regressions:

Ninepin Pt	$F = (25\,666 \times L) - 2\,219\,435$	$(r^2=0.357, n= 82, p<0.001)$
North Hope Is.	$F = (46\,419 \times L) - 3\,753\,221$	$(r^2=0.342, n= 55, p<0.001)$
East Hope Is.	$F = (12\,111 \times L) - 930\,206$	$(r^2=0.423, n= 57, p<0.001)$
Blubber Hd.	$F = (26\,220 \times L) - 2\,339\,453$	$(r^2=0.310, n= 55, p<0.001)$

where F is fecundity, in number of ova, and L is maximum shell length in mm.

From these equations it can be estimated that the length at first maturity at each site is approximately 87, 81, 77 and 90 mm at Ninepin Point, North Hope Is., East Hope Is. and Blubber Head respectively. These sizes were used as cut-off points when estimating densities of the breeding stock at each site.

3.3.2.b *Breeding Stock Removal*

At each site the density of breeding stock tended to be higher at one control than the other, while the density in the experimental areas before the removal process, generally lay between those of the two controls (Fig. 3.7). After the removal of breeding stock the densities in the experimental areas at each site were lower than either corresponding control. Analysis of variance showed that the removal of mature abalone significantly reduced their density in the experimental areas. Between sites variability and interactions between the removal process and sites were not significant (Table 3.2). Planned comparisons showed that within individual sites the removal of breeding stock significantly decreased the density of adult abalone in the experimental area at East Hope Is. and Blubber Head but that the reduction of breeding stock was not significant at North Hope Is. or Ninepin Point (Table 3.3).

Table 3.2 Anova table for a 2-factor analysis of variance comparing the density of breeding stock in the experimental areas at the four sites before the removal of breeding stock, with the density of breeding stock in the control areas.

Source	d.f.	Sum of squares	Mean Square	F-test	P
Pre. vs. Post-Removal (A)	1	1.766	1.766	18.91	<0.001
Site (B)	3	0.518	0.173	1.85	>0.10
AB	3	0.342	0.114	1.22	>0.10
Error	72	6.723	0.093		

Over all the sites, there was no significant difference between the density of breeding stock measured in the control areas and that measured in the experimental areas prior to the removal of breeding stock (Table 3.4). However, the density of breeding stock in the experimental areas after the removals was significantly lower

Figure 3.7

Results of the experimental reduction of breeding stock at Ninepin Point (NP), North Hope Is. (NH), East Hope Is. (EH), Blubber Head (BH) and for pooled data from all four sites (all sites); error bars denote 95% confidence intervals.

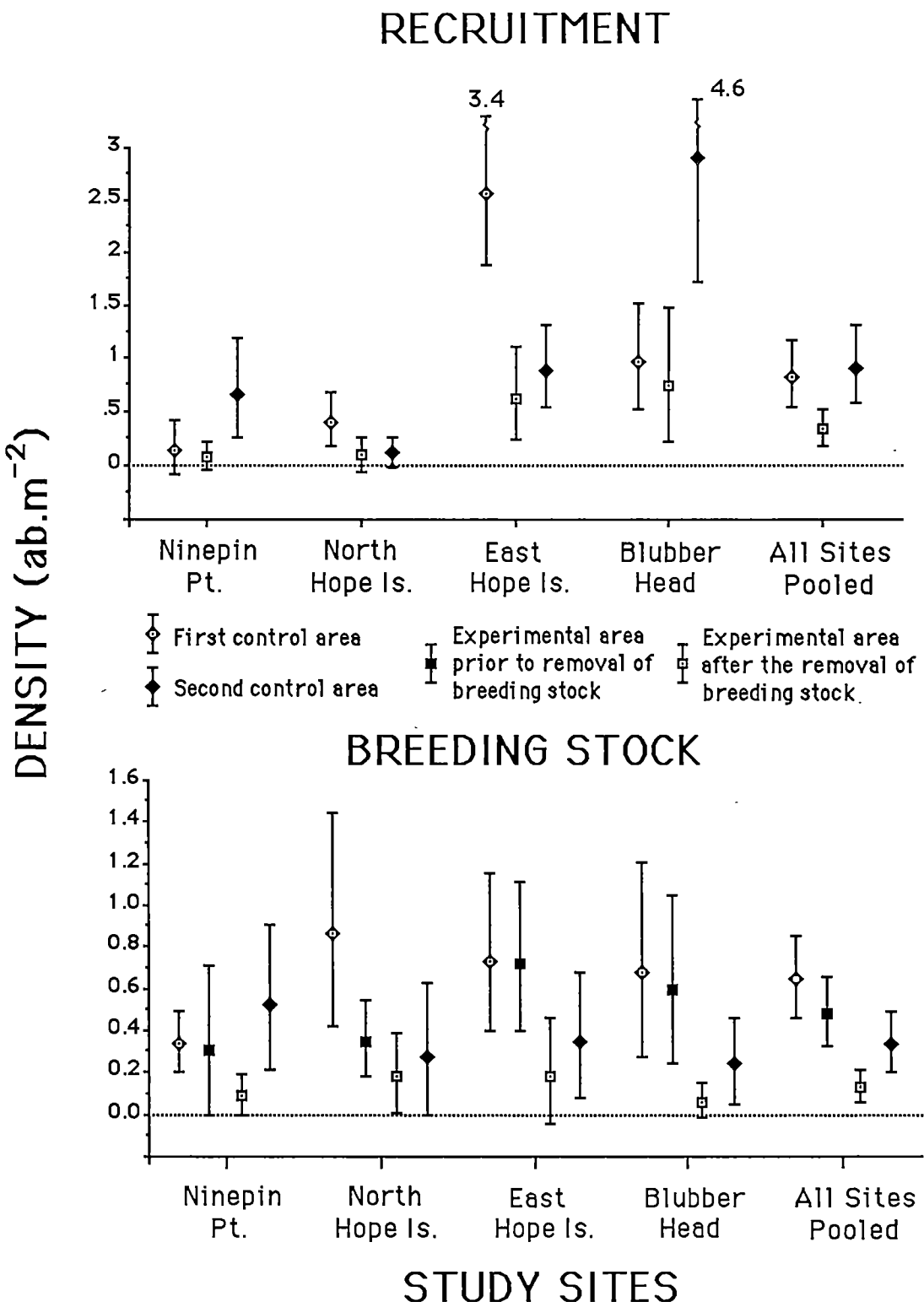


Figure 3.7

than in the controls. The difference in density between the higher density controls at each site and the lower density controls was also significant. The differences between sites were not significant.

Planned comparisons showed that, prior to the removal of breeding stock, the only significant differences in density within sites were between the higher density control of North Hope Is. and the experimental and lower density control areas, and between the higher and lower density control areas at Blubber Head (Table 3.3). Following the removal of breeding stock significant differences in density existed between the experimental area and higher density control of every site.

These tests showed that the control and experimental areas generally had similar levels of breeding stock prior to the removal of adult abalone, but that the experimental treatment significantly reduced the overall density of breeding stock in the experimental areas. The removal of breeding stock reduced the density of mature abalone in each experimental area to below that of the corresponding controls, however within particular sites this reduction was only significant when compared with the higher density control of each site.

Table 3.3 Planned comparisons testing the differences in breeding stock densities between areas within individual sites. Numbers indicate estimated F-test values (d.f.=1, 144). *denotes $p<0.05$; **denotes $p<0.01$; *** denotes $p<0.005$.

Tests	Ninepin Pt.	North Hope	East Hope	Blubber Hd.
Experimental areas				
Before vs After Removal	0.585	0.776	6.430*	7.530***
High vs Low Control	0.710	6.643**	2.972	4.184**
Experimental area before removal vs High control	1.092	4.778*	0.002	0.123
Experimental area before removal vs Low control	0.041	0.153	2.820	2.873
Experimental area after removal vs High control	4.920*	9.410***	6.660**	9.576***
Experimental area after removal vs Low control	1.892	0.239	0.734	1.101

3.3.2.c *Population Structure*

Sampling of the juvenile population immediately after the removal of breeding stock (August-September 1986) and prior to commencement of the breeding period showed that the smallest of size group of abalone present at the four sites were 8–20 mm in length with a modal length of approximately 11–15 mm (Fig. 3.8).

3.3.2.d *Sampling of Recruitment*

Sampling at the four sites in February-March 1987, showed that a new size group of abalone had been recruited to the population in each location. The newly recruited size class were 2–18 mm and had a modal length ranging from 4–12 mm between the sites (Fig. 3.8). The lengths of the newly recruited class did not overlap to any great extent with the larger size class at any location and it was possible to use 19–20 mm as a cut-off point between the newly recruited animals and the older abalone, at all sites. These cut-off points may have caused a few animals to be wrongly classified as new or old recruits but, because the cut-off points were applied uniformly within sites, it is unlikely that any bias has resulted.

At each site the density of new recruits was lower within the experimental area than in either of the control areas and analysis of variance showed that this difference was significant (Table 3.5). With the exception of the Blubber Head site, within each site the control area with the highest level of breeding stock also had the highest level of recruitment. Analysis of variance showed that unlike the density of breeding stock the density of recruitment varied significantly between sites. This contrast is probably because recruitment densities were higher than breeding stock densities while the error structure of both types of measurements were similar (Tables 3.4 & 3.5). Significant differences also existed between the controls with the highest density of recruitment at each site and those with the lowest densities (Table 3.5). Planned comparisons showed that within the individual sites significant variations in recruitment occurred at Ninepin Pt., East Hope Is. and Blubber Head (Table 3.6). At these sites the control area with the highest level of recruitment had significantly higher levels of recruitment than both the experimental and lower density control areas.

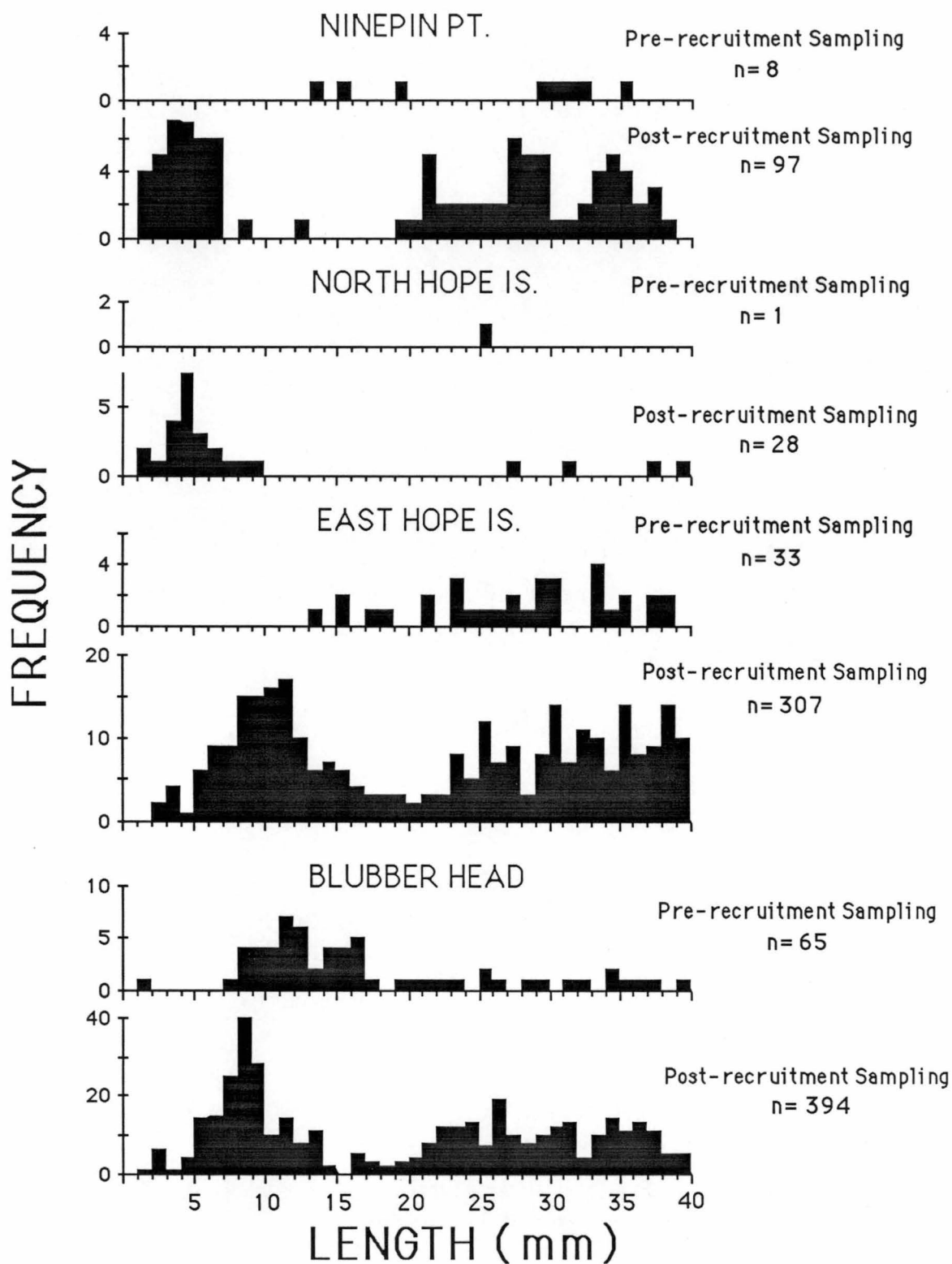


Figure 3.8 Length-frequency histograms showing 0-40 mm abalone sampled prior to recruitment (Aug.-Sept. 1986) and after recruitment (Feb.-March 1987) at the four experimental sites.

Table 3.4 Anova table for an analysis of variance comparing the density of breeding stock within and between each of the four sites.

Source	d.f.	Mean Square	F-test	P
Sites (A)	3	0.103	0.93	>0.10
Comparisons (B)				
Experimental areas before removal of breeding stock vs Controls	1	4.0E-5	6.15E-4	>0.10
Experimental areas after removal of breeding stock vs Controls	1	2.036	31.3	<0.005
High vs Low Density Controls	1	1.421	21.8	<0.005
AB Interaction	9	0.065	0.59	>0.10
Error	144	0.110		

Table 3.5 Anova table for an analysis of variance comparing the density of recruitment within and between each of the four sites.

Source	d.f.	Mean Square	F-test	P
Sites (A)	3	3.866	35.1	<0.001
Comparisons (B)				
Control vs Experimental areas	1	4.671	22.7	<0.001
High vs. Low Density Controls	1	2.884	14.0	<0.001
AB Interaction	6	0.206	1.87	>0.10
Error	108	0.110		

Table 3.6 Planned comparisons of recruitment densities between the areas within each site. Numbers show estimated F-test values (d.f.=1, 108). *denotes $p<0.05$; **denotes $p<0.01$; *** denotes $p<0.005$.

Tests	Ninepin Pt.	North Hope	East Hope	Blubber Hd.
High vs Low Controls	7.72**	2.49	18.27***	21.52***
Experimental area vs High control	8.68**	2.88	28.08***	29.60***
Experimental area vs Low control	0.16	0.02	1.05	0.64

These results show that recruitment was highly localized, with significantly different levels of recruitment occurring in some areas only 60 m apart. The fact that recruitment in the experimental areas was significantly lower than recruitment in the control areas demonstrates that the abundance of recruitment was influenced by the abundance of breeding stock.

3.3.2.e *The Relationship Between Stock and Recruitment*

This relationship can be demonstrated (Fig. 3.9) if these data are combined with those the preliminary experiment, for the Ninepin Pt. site, and measurements of stock and recruitment abundance made during February-April sampling periods at Blubber Head (v. 2.2.2). These supplementary data provide 9 extra regression points for Ninepin Pt. from the 1985/86 recruitment period, and 10 extra points for Blubber Head from the period 1983/84 to 1985/86.

With the exception of East Hope Is. the relationship between breeding stock and recruitment was significant for each of the four individual sites (Table 3.7a-d). In the case of East Hope Is. it is evident that the small number of regression points mitigated against a significant relationship being observed. These relationships suggest that approximately 60-70% of the variation observed in recruitment density can be explained on the basis of the variability of breeding stock density. When the data for all four sites were pooled a highly significant relationship between breeding

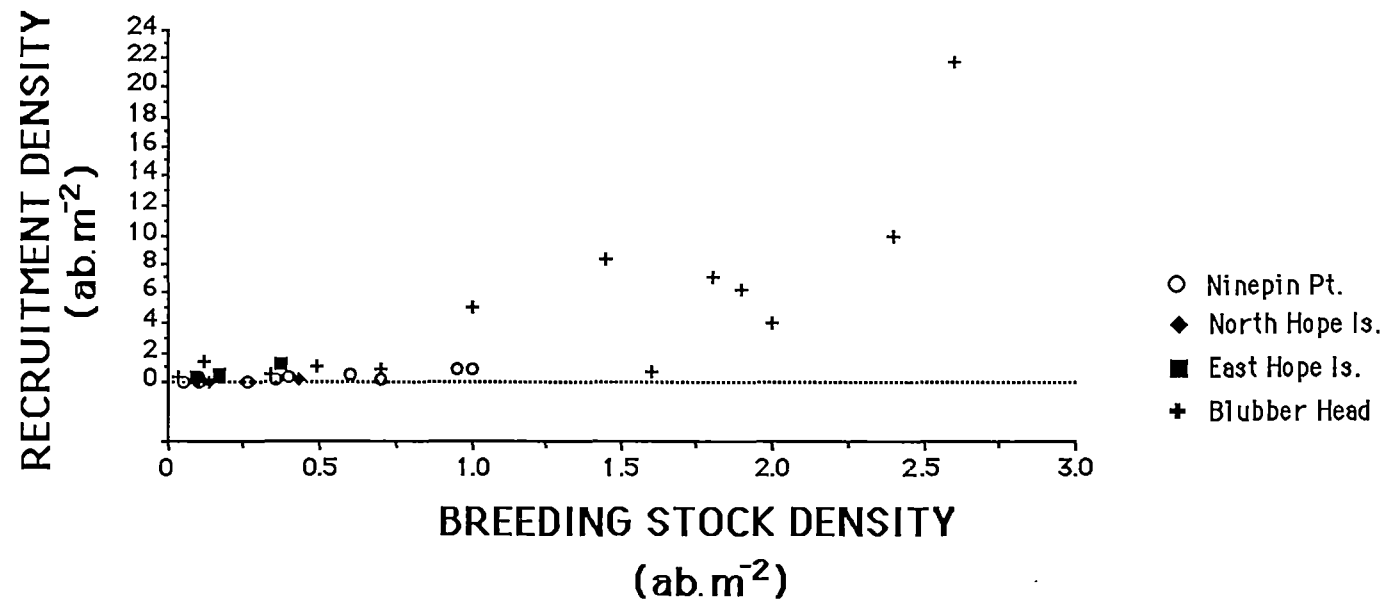


Figure 3.9
The density of recruitment plotted against the density of breeding stock for the four study sites.

stock and recruitment density was still evident (Table 3.7e), despite the inter-site variability which may have been introduced by pooling the data.

Table 3.7a Linear regression statistics for the relationship between breeding stock (X) and recruitment (Y) at Ninepin Pt.

Intercept = 0.36		Slope = 0.668		R-squared = 0.714
Source	d.f.	Sum of Squares	Mean Square	F-test
Regression	1	0.564	0.564	24.92
Residual	10	0.226	0.023	p = 5.0E-4
Total	11	0.790		

To my knowledge these data are the first estimates of a relationship between breeding stock and recruitment in haliotids to be published. Linear regressions have been fitted to this relationship simply to demonstrate that a relationship exists and should not be taken to imply that I believe this accurately represents the true nature of the relationship. In fact some form of exponential curve fits the pooled data more closely than a simple linear relationship. However because of the limitations of these data, in terms of measurement precision, restricted range of adult densities and number of regression points I believe there is little to be gained by trying to fit more complex models to this relationship.

Table 3.7b Linear regression statistics for the relationship between breeding stock (X) and recruitment (Y) at North Hope Is.

Intercept = -1.42E-5		Slope = 0.473		R-squared = 0.996
Source	d.f.	Sum of Squares	Mean Square	F-test
Regression	1	0.015	0.015	238.8
Residual	1	6.43E-5	6.43E-5	p = 0.041
Total	2	0.15		

Table 3.7c Linear regression statistics for the relationship between breeding stock (X) and recruitment (Y) at East Hope Is.

Intercept = -0.089		Slope = 3.653		R-squared = 0.975
Source	d.f.	Sum of Squares	Mean Square	F-test
Regression	1	0.538	0.538	39.0
Residual	1	0.014	0.014	p = 0.101
Total	2	0.552		

Table 3.7d Linear regression statistics for the relationship between breeding stock (X) and recruitment (Y) at Blubber Head.

Intercept = -1.42		Slope = 5.22		R-squared = 0.582
Source	d.f.	Sum of Squares	Mean Square	F-test
Regression	1	248.6	248.6	39.0
Residual	11	178.3	16.21	p = 0.0024
Total	12	426.9		

Table 3.7eLinear regression statistics for the relationship between breeding stock (X) and recruitment (Y) when the data for all sites are combined.

Intercept = -1.13		Slope = 4.82		R-squared = 0.656
Source	d.f.	Sum of Squares	Mean Square	F-test
Regression	1	397.5	397.5	55.3
Residual	29	208.5	7.189	p = 0.0001
Total	30	606.0		

3.4 GENERAL DISCUSSION

3.4.1 Patterns of Recruitment

Patterns of recruitment may arise from two causes: differential settlement or differential mortality after settlement (Keough & Downes, 1982). Connell (1985) postulated that at high settlement densities, density dependent mortality may affect

recruitment. In the present study, density dependent mortality would have had a smoothing effect, producing a pattern of recruitment more uniform than the settlement pattern. This may have reduced the likelihood of observing a relationship between spawning stock and recruitment; it can be rejected as being the cause of this relationship.

It is possible to hypothesise that some other form of differential mortality acting on the recruited juveniles is the causal agent of the observed pattern. However to do this, it is necessary to take into account the significant relationship between spawning stock density and recruitment density. Any hypothesised form of differential mortality must be inversely related to the density of adult abalone. From the literature there is no indication of any biological factor associated with adult abalone which promotes the survival of juvenile abalone after settlement. Consequently it would appear unlikely that differential mortality can explain the observed recruitment pattern and that the recruitment patterns observed reflected the abundance of settlement at each site.

Accepting that the recruitment densities observed reflect actual settlement patterns four explanatory models can be postulated to explain these patterns (Underwood 1979): (1) settlement of abalone larvae is random; (2) settlement is attracted by physical, chemical or biochemical cues independent of the adult stock; (3) settlement is attracted by physical, chemical or biochemical cues associated with the adult abalone; (4) dispersal of larvae is extremely restricted.

The first and second models are incompatible with the significant correlation that was observed between recruitment density and the density of adults. The third model cannot be discounted entirely. Abalone larvae are known to settle onto coralline algae surfaces (Shepherd & Turner 1985). It is possible that grazers such as abalone play an important role in keeping these surfaces free from epiphytes and available for settling larvae. Larvae have also been shown to settle on the slime trails of conspecifics (Seki & Kan-no 1981a). Both these factors could possibly attract larvae to settle around adult abalone and such a phenomenon has been observed in the laboratory for a number of other gastropods (see Underwood 1979). However it should also be noted that Underwood stresses that this does not necessarily happen in the natural environment.

In fact there is no evidence from any study, laboratory or field-based, that slime

trails or the presence of adult conspecifics affects settlement of haliotid larvae if clean coralline algal surfaces are available. This has only been observed in laboratory studies with larvae settling onto settlement substrates other than crustose coralline algae. It is possible that the mucous of conspecifics is only important to settling haliotid larvae when mucous rich coralline algal surfaces are not available.

At the sites used for these experiments it is extremely unlikely that mature abalone had any significant influence on the settlement sites of the larvae. In Chapter 2 it was noted that approximately 95% of the adult abalone population at Blubber Head were found in exposed sites (v. 2.4.4); this observation was confirmed during the course of these experiments with the density of mature abalone being greatly reduced (>85%) at every site by collecting abalone from the above boulder habitat. These observations suggest that adult abalone spend little time in the under boulder habitat. In contrast small abalone (<60 mm) were rarely observed on the exposed surfaces of the boulders (despite >20 h night diving) during the course of this experiment and are apparently entirely cryptic in nature (v. 2.4.4).

The crustose coralline algae on the exposed surface of the boulders tended to be overgrown with epiphytes and badly affected by silt, even before these experiments began which is in contrast to the crustose corallines on the under surfaces of the boulders in the area which showed evidence of grazing before and after the removal of breeding stock. It was on these surfaces that the small 0+ abalone (<5 mm) were usually found, suggesting that these were the settling sites. As large amounts of macroalgae other than crustose corallines were available above the boulders and these are the preferred food of *H. rubra* in this area (v. 4.3.1.e), it is improbable that the adult abalone found during the searches were grazing the coralline surfaces below the rocks or leaving many slime trails in this micro-habitat.

These observations suggest that if conspecific abalone have a role in conditioning settlement sites it is probably the juveniles, not the adults, which are most important. Consequently, it is improbable that the observed recruitment patterns resulted from settlement being attracted by cues associated with adult abalone. This conclusion is supported by Shepherd and Turner (1985) who, on the basis of a detailed field study, discounted the likelihood of abalone larvae being attracted to or by conspecific adults.

The final model which can explain the settlement pattern inferred by this study is

that abalone larval dispersal at the study site was extremely restricted. This explanation implies that significant amounts of larvae did not travel into the removal areas from the spawning stock known to have been outside the area, a distance of only 15-30 m. The literature for haliotids assumes that abalone larvae are pelagic (Mottett 1978; Fedorenko & Sprout 1982; Tegner & Butler 1985a), swimming to the surface after hatching. Matthews and Volframs (1978) studied a body of water at the northern end of the D'Entrecasteaux Channel and showed that in depths <10 m water movement is primarily wind driven. From the relationship derived by that study between wind strength, depth and water movement, and from meteorological data (Aust. Dept. Sci., unpubl. data), it is possible to estimate the magnitude of water movements in the experimental area during the September to November 1985 spawning as approximately 0.005–0.038 m.s⁻¹. The movement can effectively be considered unidirectional for time periods of 48-96 h (Matthews & Volframs 1978). This would have resulted in a gross movement of between 430 and 3300 m for every 24 h period abalone larvae spent in the water column, depending on the depth at which they occurred. The gross distance moved by a cell of water indicates a magnitude of mixing and dispersal, for pelagic larvae, that is incompatible with the localized reduction in settlement observed in this experiment. Clearly, the assumption of a pelagic larval life for *H. rubra* is not supported by the settlement pattern inferred by this study. Considering the magnitude of the water movement, the inverse of this assumption is suggested by these results. That is, that haliotid larvae avoid dispersal.

3.4.2 Re-evaluation of haliotid biology and behaviour

The assumption that abalone larvae are pelagic in the natural environment rather than demersal is based solely on laboratory observations of haliotid larvae, and what is apparently the prevailing dogma in marine invertebrate zoology, that if larvae can swim they are pelagic. Under laboratory conditions abalone trochophores are positively phototactic and swim slowly towards the surface (Ino 1952; Leighton 1974; Yano & Ogawa 1977; Tanaka 1978). Late stage veligers exhibit 'tumbling behaviour', in which large numbers assemble in vertical columns and at irregular intervals spontaneously tumble to the bottom of the tank and disperse (Leighton 1972; Grant 1981; J. Grant & C.E. Sumner, pers. comm.). Mariculturists take

advantage of these behaviour patterns by using surface collection techniques when transferring larvae between tanks (Ebert & Houk 1984). Under laboratory conditions settlement of larvae generally occurs between 3-11 days post fertilization, depending on temperature (Ino 1952; Leighton 1974; Ebert & Houk 1984). These observations have all been made during mariculture research programs and no controlled experiments have been published which test their accuracy or relevance to natural conditions. Instead the applicability of these observations to the natural environment has been assumed, and they have been taken to indicate that naturally occurring abalone larvae are pelagic, having a dispersal phase before becoming competent to settle (precompetent phase) equivalent to the time taken to settle in the laboratory (Mottett 1978; Fedorenko & Sprout 1982; Sluczanowski 1984; Tegner & Butler 1985a).

However there is no certainty that such an assumption can be made (Underwood, 1979). Firstly, the preferred settlement conditions for abalone are still poorly understood and can only be crudely approximated in the laboratory (T. Dix, pers. comm.; J. Grant, pers. comm.). It is known that when faced with less than optimal settlement conditions invertebrate larvae postpone settlement (Thorson 1950). It has also been shown that the discrimination of the larvae choosing settlement substrates decreases as larval life is prolonged (Knight-Jones 1953). Because of this, the time from fertilization to settlement observed in the laboratory may be a gross over estimate of the average length of larval life in the natural environment, where optimal settlement conditions occur. These estimates of the length of abalone larval life derived from laboratory observations should be regarded as estimates of the maximum length of larval life rather than the minimum.

The minimum possible larval life length is actually the time required by the larvae to become physiologically capable of settling (Strathmann *et al.* 1981) and this is the correct definition of the precompetent phase (Jackson & Strathmann 1981). For abalone, this is when the third tubule forms on the cephalic tentacles, and the ctenidium and first epipodial tentacle appear within the larval shell (Grant 1981; Seki & Kan-no 1981b). For *H. rubra* the length of the precompetent phase is about 106 h at 16°C (J. Grant & C.E. Sumner, pers. comm.) although settlement in the laboratory does not normally occur until about 142 h post fertilization. However even this does not give a true indication of what may be the minimum possible time

available for dispersion. To estimate this it is necessary to consider the proportion of the precompetent phase during which the larvae are physiologically forced to swim freely. Abalone eggs are considerably heavier than water (Ino 1952; Grant 1981) and if dispersal occurs it is unlikely to occur before the trochophore hatch. In addition abalone larvae are able to stop swimming and explore settlement surfaces by creeping, from the time the two snout protuberances are formed (Seki & Kan-no 1981b). For *H. rubra* the time between hatching and being capable of movement by creeping rather than swimming is only about 43 h at 16°C (J. Grant & C.E. Sumner, pers. comm.).

The second difficulty with assuming that the behaviour of larvae in the laboratory is the same as behaviour in the natural environment is that the simple, smooth, sterile laboratory tanks in which the larvae are held are totally divorced from the biologically and physically complex bottom on which abalone naturally occur. Also, the densities at which the larvae are held are probably several orders of magnitude higher than those found naturally (T. Dix, pers. comm.; J. Grant, pers. comm.; L. Tong, pers. comm.). In these conditions it cannot be assumed that larval behaviour is normal. Even if this assumption is made, the importance of stereotyped behaviour may be lessened by numerous conditions in the field (Moore 1975; Young & Chia 1982). It is likely that if the behaviour of cultured larvae corresponds to the behaviour of larvae in the natural environment, then it may correspond to the behaviour of larvae that have hatched in smooth, simple conditions such as the middle of a large sandy area. It has been demonstrated that invertebrate larvae are capable of a number of behaviour patterns stimulated by different settlement prospects (Harrigan 1972; Young & Chia 1982). A possible hypothesis is that larvae in the laboratory are attempting to disperse widely because they do not receive the cues which indicate the proximity of appropriate settling sites, while larvae that detect these cues may react in a way which avoids or minimizes dispersal.

Restricted dispersal of larvae is favoured amongst benthic marine invertebrates when the resources they require are uniformly available (Menge 1975) and relatively free of temporal variation (Palmer & Strathmann 1981). In this situation larvae that disperse have a lower probability of finding suitable habitats than non-dispersing larvae and face greater risks while they search (Sebens 1983). After settlement in a suitable habitat there is little compensation for this cost as the habitats chosen by

both the dispersing and non-dispersing individuals animal are equally likely to continue providing the resources needed (Palmer & Strathmann 1981). No published evidence exists to suggest that adult abalone reduce the suitability of habitat for larvae or juveniles, indicating that the resources required by abalone larvae are as likely to be available locally as further afield. In addition, the kelp communities in which abalone are found are temporally stable (Dayton *et al.*, 1984; Tegner, in press). Thus the resources required by abalone are both uniformly available and temporally stable. As a consequence, it should be expected that abalone will have evolved morphological and behavioural adaptations which will restrict larval dispersal.

For morphological reasons, the primitive archaeogastropoda cannot easily produce complex egg capsules nor undertake internal fertilization (Yonge 1947). Therefore, direct development benthic egg capsules, in which larvae pass through all development stages, and viviparity, the two most frequent means of restricting larval dispersion (Thorson 1950; Mileikovsky 1971), are not commonly found in Archaeogastropoda (Underwood 1979). Underwood (1979) hypothesised that in small gastropods denied these strategies and pelagic larvae by their extremely small body size, would be forced to develop by non-dispersal lecithotrophy. Similarly, it can be hypothesised that archaeogastropods such as haliotids, ecologically favoured by non-dispersal but morphologically constrained from evolving direct development or viviparity, are also likely to develop this form of dermersal development larvae.

Circumstantial evidence exists suggesting that abalone have behavioural adaptations which aid in restricting larval dispersal. For example, the only published observation, of wide-scale spawning of haliotids in the natural environment occurred in calm conditions and after several days of very calm weather (Breen & Adkins 1980). From anecdotal information provided by commercial divers in Tasmania, N.S.W and South Australia, *H. rubra* also appears to spawn during extremely calm weather. These observations suggest that abalone populations possibly select conditions of low water movement for spawning, adaptive behaviour which would minimize dispersion of gametes, eggs and larvae. *H. rubra* maintains its gonads in a ripe state for long periods (Harrison & Grant 1971; McShane *et al.* 1986), as do many haliotids (Mottett 1978), and this may enable them to coincide spawning with short irregular periods of low water movement. A

similar phenomenon has been observed in the limpet *Cellana radians* (Gmelin) which coincides spawning with localized conditions of water movement (Creese & Ballantine 1983), although for this limpet the required condition is high water movement. A number of haliotid species have been found to have variable spawning times (Newman 1967; Poore 1973; Shepherd & Laws 1974; Shepherd *et al.* 1985). More specifically, several studies have observed that conspecific abalone populations separated by short distances spawn at different times (Webber & Giese 1969; Hayashi 1980b); this has also been observed for *H. rubra* (McShane *et al.* 1986). These observations suggest that locally specific cues such as water movement, may be important in stimulating spawning in haliotids. This could explain why the role of more universal cues such as water temperature and day length are so ambiguous (Webber & Giese 1969; Shepherd & Laws 1974; Shepherd *et al.* 1985; McShane *et al.* 1986).

This hypothesis is consistent with the results of the current study when spawning occurred between 18 and 29 September 1985. During this time, a three day period (21-23 September) occurred when winds were generally offshore and lighter (2.3 m.s^{-1}) than the average wind speed of September (7.6 m.s^{-1}), a highly significant difference ($t=9.17$; $\text{d.f.}=198$; $p<0.001$; Aust. Dept. Sci., unpubl. data). It is possible that the spawning of the abalone in the study area coincided with this calm weather.

The eggs produced by haliotids are considerably heavier than water and if released over boulder substrate, can be expected to sink and roll down into the substrate before hatching. Lodging the eggs within the substrate would prevent the eggs being rolled across sandy substratum away from reef habitat, and ensure that larvae begin their life in substrate suitable for settlement. The behaviour observed by Breen and Adkins (1980) and supported by the observations of Quayle (1971), of spawning abalone climbing up onto kelp and prominent points of the substratum before releasing ova is also reported by commercial divers for *H. rubra*. As abalone are often found on the edge of rocky substrate and sand, where drifting kelp accumulates (Shepherd 1973), this behaviour in calm water conditions could cause the breeding abalone to move upwards away from sandy areas maximizing the probability that their eggs fall on to, and lodge in hard substrate, rather than falling on to sandy substrate.

Yano and Ogawa (1977) studied the behaviour of the larvae of *H. gigantea* under controlled laboratory conditions and found that the trochophore are positively phototactic and negatively geotactic. Their study found that 75 h after hatching 80% of the larvae were still in the top 10 cm of the water column. Tegner and Butler (1985a) used these results to imply that in the natural environment haliotid trochophores are generally positively phototactic and swim to the surface of the water mass where they remain for up to 75 h. However, this conflicts with the results of Tanaka (1978) who, while confirming that 3 and 5 d-old larvae (post fertilization) of the same species are positively phototactic, found them to be most abundant in the bottom layer of still water laboratory tanks.

In the laboratory, the trochophores of *H. rubra* swim freely for about 10 h at 16°C; however they stop swimming and sink if they encounter hard surfaces or turbulence (J. Grant, pers. comm.; C.E. Sumner, pers. comm.). If this behaviour also occurs in the natural environment it is extremely uncertain as to whether the trochophore normally swim to the surface of the water mass, or even move out of the interstitial spaces within reefs. An alternative hypothesis is that being positively phototactic helps the larvae to orientate within the substratum. This could enable the larvae to move from deep within the substratum where the eggs may have lodged towards the lighter upper boulder layers where suitable settlement sites (crustose coralline algae) are most abundant. It is possible that the behaviour observed in the laboratory, whereby larvae stop swimming and sink if they encounter water movements, enables the larvae to avoid leaving the protected sub-boulder habitats.

Recent studies conducted by McShane *et al.* (1988) in Victoria suggest that there would be strong selection pressure on *H. rubra* to develop larvae capable of avoiding dispersal. By modelling water movement within and around abalone reefs they found that larvae that entered the water column would be flushed from reefs and have almost no chance of encountering any other suitable habitats during their larval life.

In addition to being consistent with the results of this experiment, the hypothesis that haliotid larvae are adapted to avoid dispersal, also offers an explanation for the observations of Breen and Adkins (1980) who found no abalone larvae, despite towing a plankton net over a known spawning site 2 and 3 days after the spawning. It also explains the findings of Tomita *et al.* (1977) who, by using a plankton

pump, found only small numbers of larvae in 6 of 19 samples. In only two of these samples were the larvae more numerous in the surface layer than the bottom layer and both these latter samples were taken from depths <3 m. This hypothesis is also consistent with the observation reported in Sluczanowski (1984) that, in an isolated substock, a positive relationship had been found between the biomass of fecund abalone and the recruitment of 1+ animals. Restricted dispersal patterns for haliotid larvae are also consistent with the high levels of inbreeding observed in haliotid populations (Fujino 1978; Fujio *et al.*, 1983).

3.6 GENERAL DISCUSSION AND CONCLUSIONS

The experimental design of the experiment described here makes it impossible to categorically distinguish between the effect of removing the adult abalone and the effect of removing their potential reproductive capacity. Knowlton and Keller (1986), in their study of the larval dispersal of an alpheid shrimp, were able to distinguish between the effect of the physical and reproductive presence of the adults by using sterilized adult shrimp. Before the role of these differing factors can be determined absolutely for haliotids it will be necessary to develop a similar capability with these species. To my knowledge no technique for sterilizing adult abalone exists, but in this respect the study of Tong *et al.* (1987) has considerable potential. They produced competent haliotid veligers in a hatchery and introduced them directly into the natural environment. This suggests the possibility of using eggs fertilized in the hatchery to manipulate the breeding potential of abalone independently of the density of mature abalone. Such techniques may make possible an experiment capable of determining whether the relationship between breeding stock and recruitment is due to gregarious recruitment around conspecific adults or to localized larval dispersal.

Whichever underlying cause results in the relationship between breeding stock and recruitment, the fact that this relationship exists is of relevance to the managers of haliotid fisheries. Clearly these results show that for populations of *H. rubra* stock and recruitment relationships must be considered on a spatial scale as small as 10–100 m.

CHAPTER 4

A STUDY OF AN EXPLOITED POPULATION OF

HALIOTIS RUBRA.

4.1 INTRODUCTION

The broad aim of this segment of the study was to complement Chapter 2, which described the general biology of an abalone population prior to its recruitment into the fishery. In this chapter I describe the general biology of the exploited or recruited portion of an abalone population. I examine the general biology and behaviour of the exploited population, including growth, feeding, maturity, age structure of the population and movement. In later chapters I consider how the biology of the species is likely to interact with the fishery.

I decided that the most appropriate method for this broad-brush type of study would be an extended tagging study supported by supplementary sampling programs. The final recapture of this tagging study took place as part of a fishdown experiment using commercial divers which is described more fully in Chapter 5. It will be discussed in this chapter only as a part of the tagging study.

4.2 METHODS

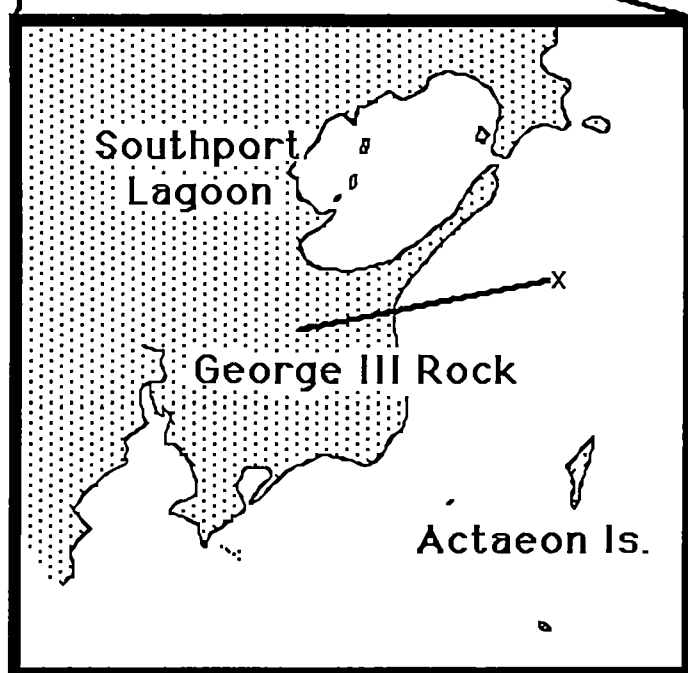
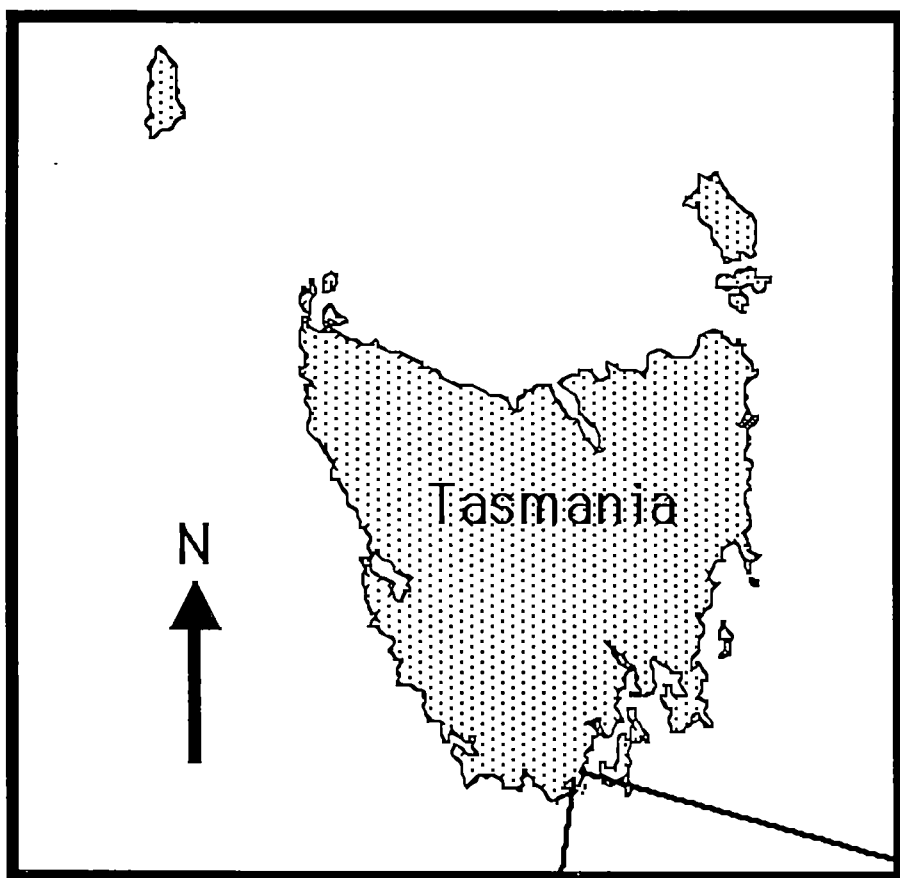
4.2.1 Study Site

The commercial fishermen in the south-east of Tasmania were asked to indicate an easily identifiable, discrete area of commercial abalone reef which they were prepared to close to all fishing for the duration of the study. It was stressed that the area should be representative of normal commercially fished areas. They nominated George III Rock (43°31'S, 146°58'E.), a relatively exposed reef in the extreme south-east of Tasmania (Fig. 4.1). Subsequent inquiry indicated that at least four commercial fishermen fished this area on a regular basis before the area was closed to fishing in April 1984.

George III Rock is an area of reef approximately 850 m long and 900 m wide with a total area of *c.* 350 000 m² (Fig. 4.2). The actual rock from which the reef takes its name, is a protuberance of bedrock which forms the centre of the reef (2-4 m) and over which the sea regularly breaks. This rock is surrounded by approximately 40 000 m² of extremely broken bottom which consists primarily of sheets of dolerite bedrock overlaid with several layers of boulders. These boulders are large with diameters of 1-5 m. Outside this central area, in depths of 10-18 m, the bottom is less complex being composed mainly of scattered boulders sitting on the bedrock sheet or on sand. The reef runs into sand on all sides at a depth of approximately 15-18 m and the area is surrounded by large expanse of unbroken sand, the nearest reefs being 2-3 km distance.

The dominant kelp species found on the site are string kelp (*Macrocystis pyrifera*),

Figure 4.1
The location of George III Rock.



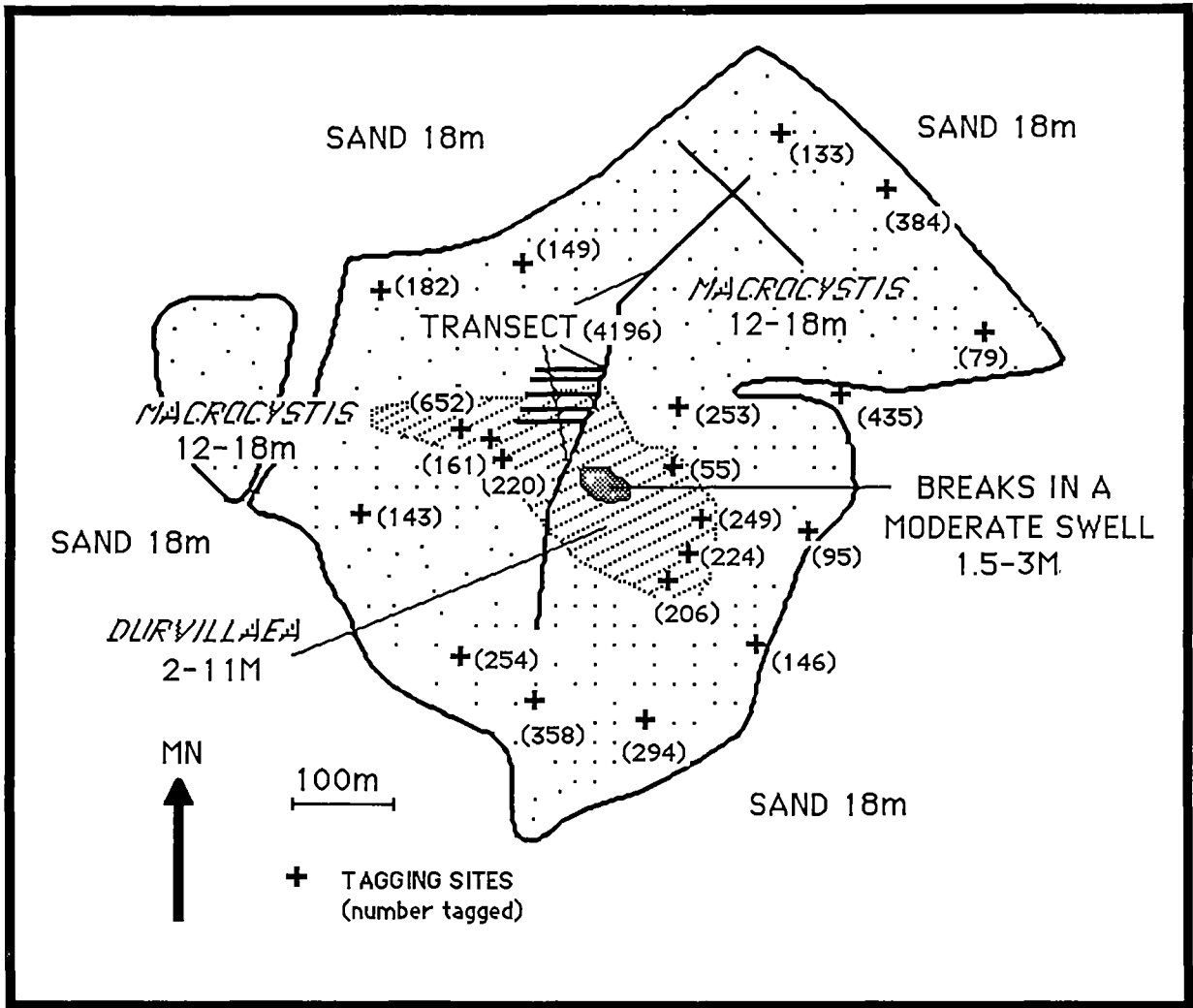


Figure 4.2
 A map of George III Rock showing: the approximate dimensions, distribution of the major habitats, depths, layout of the transect, location of tag releases and the number of abalone released at each location.

bull kelp (*Durvillaea potatorum*) and crayweed (*Phyllospora comosa*). These kelps mark the major habitats found on the reef. The most extensive habitat is dominated by the string kelp and is found at depths >11 m. This habitat occupies approximately 90% of the reef area and it is characterised by its dense understory turf of small (2-5 cm) fleshy red algae of the genera *Plocamium*. Bull kelp dominates the other major habitat in depths <11 m. This habitat lacks the fleshy red algae and the understory is dominated instead by encrusting coralline algae. Separating the two major habitats in depths of 9-11 m is a third intermediate habitat characterized by *Phyllospora comosa*. This habitat forms a narrow band (20–30 m wide) around the shallow area of the reef.

4.2.2 Supplementary Studies

4.2.2.a Population Structure

Anaesthetic sampling, using the technique described by Prince and Ford (1985), was conducted in June 1987 to sample the juvenile population at the research site. In June 1987 research divers also made a collection of all the emergent abalone that could be found in a 15 m x 15 m area of the *Durvillaea* habitat to obtain an independent measure of the density of legal size abalone prior to the fishdown experiment as well as a profile of the age composition of the emergent population. The abalone collected at this time were measured for length, and aged using the techniques documented by Prince *et al.* (1988).

A Gompertz growth equation was fitted to the length at age data derived during the June 1987 samples using the micro-computer program FISHPARM of Prager *et al.* (1987).

4.2.2.b Reproductive and Feeding Studies

Samples of abalone were collected periodically (when weather and other field commitments allowed) during 1985-1987 for feeding and reproductive studies. On each occasion samples were collected from the three different habitats so that diets could be compared. Animals were collected early in the morning of each sampling day and returned to the laboratory where they were weighed and dissected. The foot muscle was weighed and the visceral mass was preserved in 10% formalin. Gonadasomic indices were assessed as described in Chapter 2 using the preserved visceral mass. Preserved stomach contents were removed from the viscera for a study of diet. Stomach contents were drained and weighed before examination to estimate a gut fullness index. This index was estimated as the weight of the stomach contents as a percentage of the foot muscle weight.

The techniques used to examine diet follow Poore (1972c). The contents of each stomach were stirred into water and placed in a petri dish with a diameter of 15 cm. The relative abundance of items in the diet was scored by identifying algal fragments on 25 evenly spaced points marked on the base of the petri dish. Where possible algal fragments were identified to a species level; however this was not possible for the large brown algae as the fragments of phaeophytes constituted such small portions of these plants and they rarely contained differentiated and identifiable structures.

Logarithmic selectivity indices have been calculated using the formula:

$$\text{selectivity index} = \log (D/H) \quad \text{eq. 4.1}$$

where D is the percentage occurrence of the food item in the diet and H is the percentage occurrence of the food item in the habitat (Berg 1979).

4.2.3 Tagging Studies

4.2.3.a Overall Design

This study was structured around a large multi-purpose tagging program which involved two 'nested' tagging studies. The first of these was a multiple release-recapture study conducted around a permanent transect within the research site. Releases around the transect, together with other releases throughout the site, formed the basis of the second tagging study: a multiple release–single recapture study incorporating the entire study area. Because of the limited knowledge of movements, this broad ranging approach was used so as to obtain the wide range of information required from the study.

At no time during this tagging study was the substratum disturbed to find abalone, so it can be assumed, therefore, that only non-cryptic or emergent abalone have been tagged and recovered. Consequently, all the results of this chapter, unless specifically stated, apply to the emergent portion of the abalone population at George III Rock and should not be applied more generally.

4.2.3.b Tagging Technique

The tag used was developed for this study and consisted of a circular laminated numbered disc (14 mm in diameter) with a central hole and a small (6.2 x 4.8 mm) nylon rivet (Fig. 4.3). The rivets are applied mechanically by placing the jaw of a rivet into a respiratory pore, and then forcing the tail of the rivet through the head, expanding the jaws to hold the tag in place. This was accomplished with a specially designed tag applicator and tag holder. Tagging could be conducted in or out of the water equally

easily.

Tags were affixed to the respiratory pore furthest from the growing margin whenever possible. This is the oldest active respiratory pore on any abalone and the first to be sealed with nacre. The application of tags to this pore should have enhanced tag retention and reduce the possibility of the tag interfering with the animal.

4.2.4 Multiple Release - Recapture Study

4.2.4.a *Field Work Techniques*

The multiple release-recapture phase of this study provided information about abalone movement that would be accurate on a scale of 5-10 m. A 675 m long permanent transect of old 11 mm trawl cable was laid in the research area down the long access of the reef (approximately north-south) and running through the complete range of habitats and depths. A number of permanent mooring sites were established on the transect and distances along the transect measured and marked in order to provide permanent reference points (Fig. 4.2). The difficulty with this approach is that estimates of the distance moved by abalone, are biased downward by the movement of animals out of the area being searched. To extend the scope of this study a permanent 60 x 60 m grid was established by laying out 5 parallel 60 m lengths of chain (Fig. 4.4). These chains ran perpendicular to the main transect on the north-western side of the site; spanning the three major habitats within the reef. The rationale of this structure was that if abalone movement was found to be extremely restricted (0-5 m) then the chains could be treated as extensions of the transect while if movement was slightly greater 5-20 m the grid structure would be necessary to provide relatively unbiased estimates of distance moved.

Research divers completed a total of six episodes of abalone tagging and/or recapturing around the transect from February 1985 to March 1987 (Table 4.1). During February and November 1985, October 1986, and March 1987 the entire length of the transect out to a distance of 10 m on either side was searched and all the abalone found were recorded, measured, and tagged if necessary. During May 1985 a standard search of the transect was conducted and the position and length of all tagged abalone was measured; however no tagging took place. In March 1986 a similar search took place, but during this search only a small number of abalone were tagged and released.

Figure 4.3
Tags and tagging equipment developed for this study.

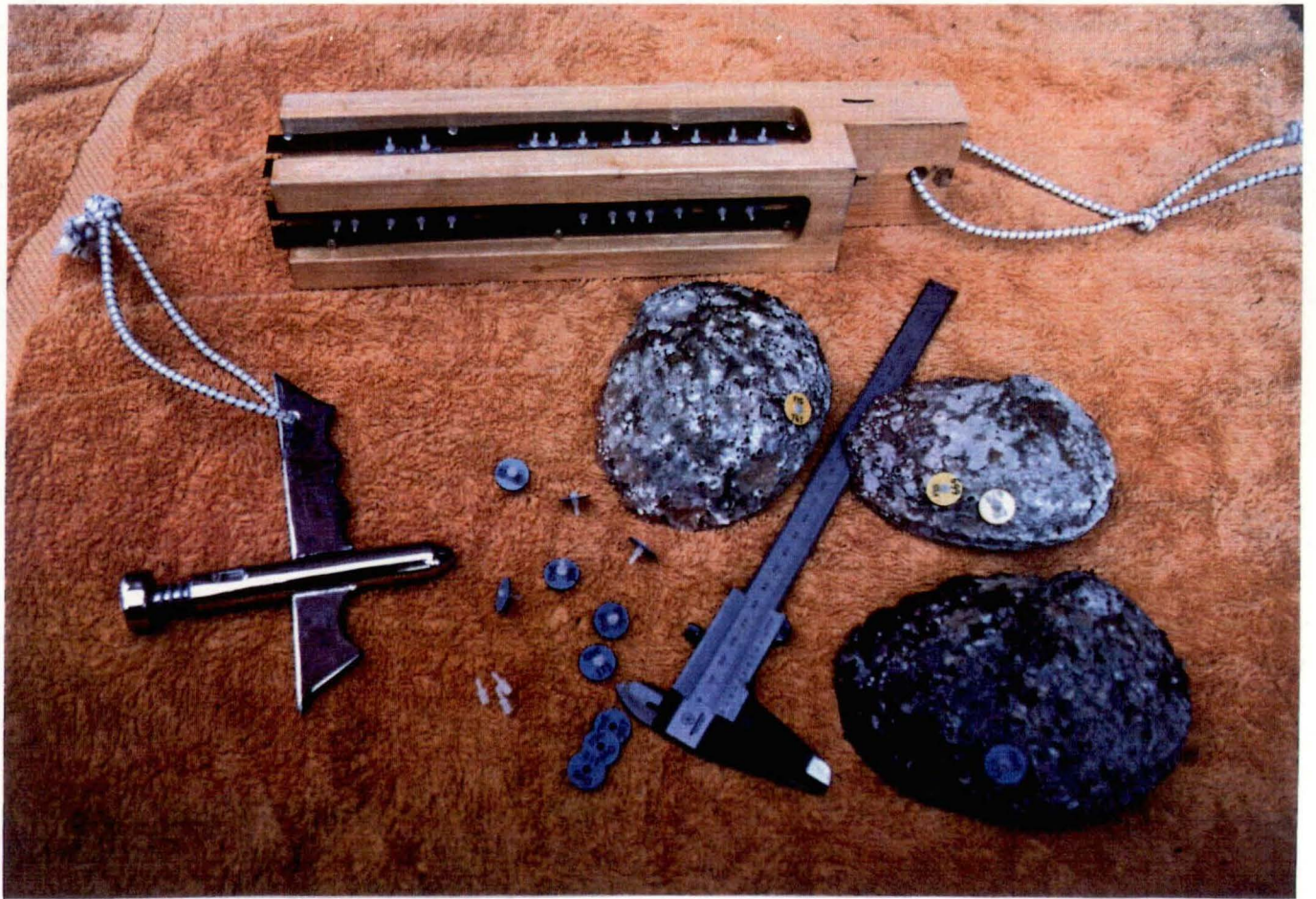


Figure 4.3

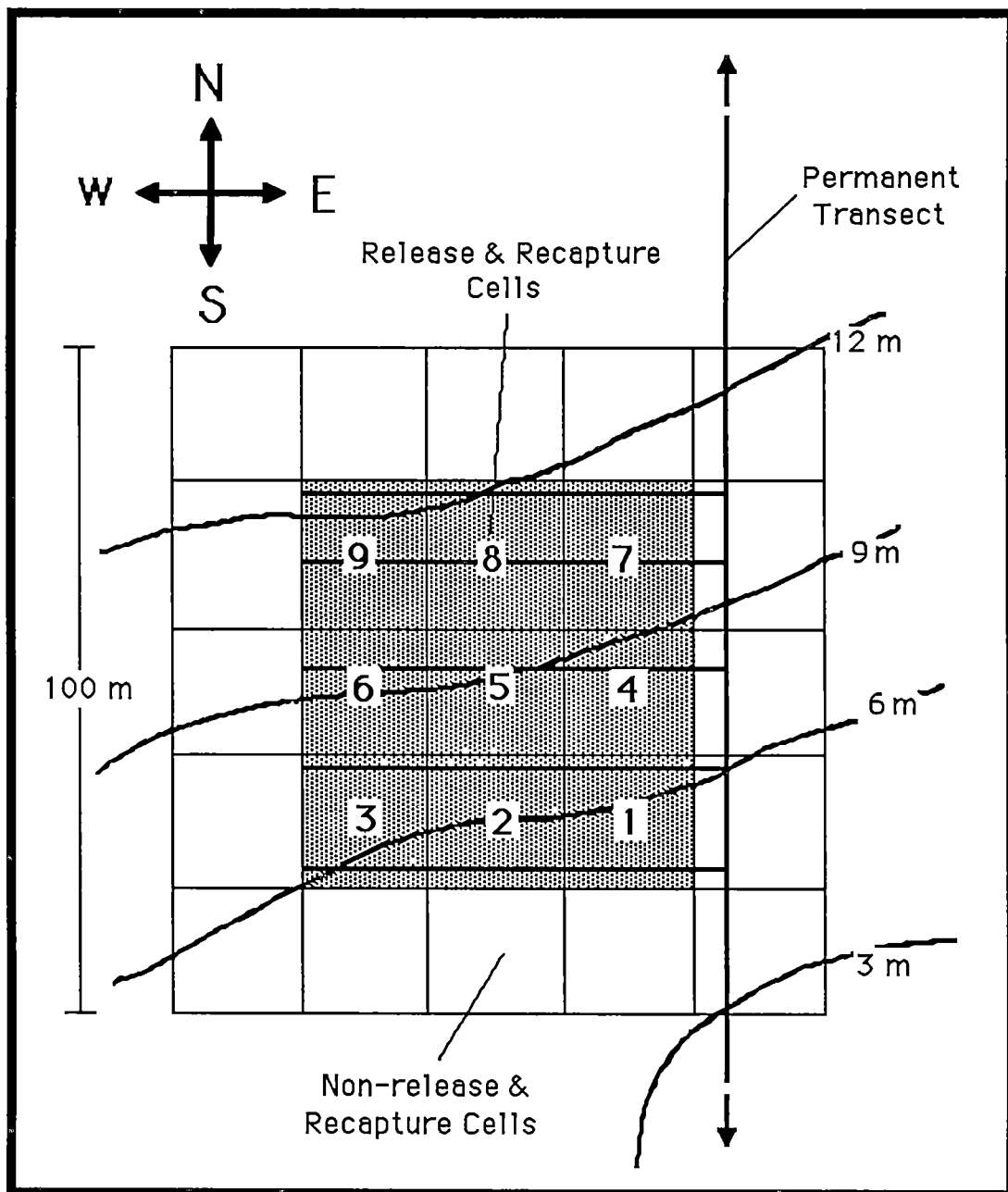


Figure 4.4

A detailed diagram of the section of the permanent transect made up of 5 parallel chains laid to form 60 x 60 m grid. Super-imposed over the actual transect is the grid structure conceptualized for use with the iterative model used to analyse the multiple release and recapture data (v.4.3.2.b.a).

Table 4.1 Details (numbers, dates, locations) of tag releases and recaptures at George III Rock.

Date	Activity	Type of Tagging		Location	
		<i>In situ</i>	Boat	On Transect	Off Transect
Feb. 1985	Release Only	*	*	*	
May 1985	Recapt. Only			*	
Nov. 1985	Rel. & Recapt.	*		*	
Mar. 1985	Recapt. & Minor Rel.	*		*	
Jun. 1986	Release Only		*		*
Oct. 1986	Rel. & Recapt.	*	*	*	*
Mar. 1987	Rel. & Recapt.	*	*	*	*
Jul. 1987	Recapt. Only			*	*

With the exception of the initial release, all tagging and recapture around the transect took place underwater. The abalone were left attached to the reef if possible, and replaced exactly on their attachment sites if this was not possible. Of the abalone tagged and recaptured in this way, 53 and 82% respectively, did not have their attachment broken. During the first release around the transect approximately 70% of the animals released were tagged in the boat (see below for a detailed description of this procedure) to provide comparison between the two methods of tagging.

During release and recapture the location of each abalone was noted as a distance along the transect (± 2.5 m) and a distance to either side of the transect (± 0.25 m). The maximum length was also measured to the nearest 1 mm with Vernier calipers and recorded. Whether or not an abalone was removed from the substrate during tagging, or taken to the boat for tagging was noted as was the incidence of accidental wounding, tag number and respiratory pore to which the tag was attached.

4.2.4.b Analysis

4.3.2.b.a An Iterative Model Analyzing Multiple-Release-Recapture Data.

A simple iterative model was constructed to analyse the multiple release–recapture data collected from the 60 x 60 m grid within the transect (Fig. 4.2). Only releases and recaptures made within the confines of the grid were used in this analysis. Abalone involved in this analysis were released in February 1985, November 1985, March 1986

and October 1986 (Table 4.2). Recapture searches were conducted as part of each release, with the obvious exception of the first release. Additional recapture searches were also made in March 1985, when no abalone were released, and in March 1987 when abalone were released but not for recapture within this analysis. The March 1986 release was to have been purely a recapture search, however a few animals were released and so this has been included as a release and recapture.

Table 4.2 Dates when tagging and/or recapture took place within the grid structure at George III Rock, numbers indicate the number of abalone tagged within each grid cell during each search.

Date	Grid Cell Number								
	1	2	3	4	5	6	7	8	9
Feb. 1985	35	35	54	48	42	38	47	75	29
May 1985	0	0	0	0	0	0	0	0	0
Nov. 1985	35	60	98	43	28	29	52	20	21
Mar. 1986	1	4	1	1	1	1	12	3	7
Oct. 1986	65	70	69	36	42	55	65	28	65
Mar. 1987	41	48	87	21	47	70	33	22	43

For the purpose of the analytical model the transect grid was conceptualized as a square (Fig. 4.4) made up of 9 cells each 20 x 20 m, which are the central cells of a larger 5 x 5 cell square. Releases and recaptures only took place within the central cells (1-9); however the model follows the movement of abalone within all 25 cells of this imagined grid structure.

Within the model it is assumed that the number of tagged abalone observed during any search ($ObsN_t$) is determined by:

- a. The initial number of tagged abalone released ($N_{rel.}$).
- b. Initial loss of tags and mortality ($Loss_{Init.}$) resulting from the tagging process so that:

$$N_0 = N_{rel} - (N_{rel} \times Loss_{Init.}) \qquad \text{eq. 4.2}$$

where N_0 is the number of live abalone with tags at the completion of the tagging process ($t=0$). The two components of initial loss, initial tag loss and tagging mortality are not distinguishable by the model and have been lumped together.

- c. Continuing tag loss and natural mortality. These two parameters have also been

lumped together as the model cannot distinguish between them. This value is modelled as a fixed proportion of the tagged abalone present in any month:

$$N_t = N_{t-1} - (N_{t-1} \times \text{Loss}_{\text{Cont.}}) \quad \text{eq. 4.3}$$

where N_t is the number of tagged abalone alive at time = t months and $\text{Loss}_{\text{Cont.}}$ is the proportion that die or lose tags during any month.

d. The movement of tagged abalone. Movement has been assumed to be a diffusion process. Diffusion is only modeled horizontally and vertically out of each cell. The lack of a direct diagonal component is not considered to be important within the error structure of these data. In the initial version of the model the rate of diffusion was directional but not cell specific:

$$N_{\text{dir.}} = N_t \times \text{Mov}_{\text{dir.}} \quad \text{eq. 4.4}$$

where $N_{\text{dir.}}$ is the number of abalone moving in any given direction during any month, N_t is the number of abalone present in month t and $\text{Mov}_{\text{dir.}}$ is the probability of movement in a given direction during any month. Within this study the four different directions have been designated north, south, east and west, in loose accordance with the orientation of the grid (Fig. 4.2).

e. The probability that an abalone inside the grid will be sighted by a searching diver. For the initial estimates this been assumed to be some fixed probability (ProbObs):

$$\text{Obs}N_t = N_t \times \text{ProbObs} \quad \text{eq. 4.5}$$

Using any given set of values for the above parameters the model predicts the decay and dispersion of abalone released in each cell of the central 3 x 3 grid and, by calculating a sum of squares, compares these values with the observed recapture data.

The best values for the parameters have been fitted by searching iteratively for the combination of values which gives the least sum of squares value. Approximate confidence intervals for estimates derived in this way have been calculated using the method of Draper and Smith (1966). A listing of a modified version of this program is contained in Appendix 2.

4.3.2.b.b An Iterative Model for Estimating the Probability of Recapture.

The probability of sighting an abalone during a search was also estimated independently of the dynamics model with a second iterative model. This model used the recapture records of animals released in February-March 1985 and October-November 1985 and recaptured in subsequent searches. Only releases and recaptures made within the 60 x 60 m grid defined for the abalone population model were used. The major

assumption of this model is that if an animal was recaptured in a particular search it was assumed to have been available for recapture within the grid during the preceding searches.

Using this assumption, as well as the number of animals recaptured in any recapture from a particular release, the model predicts, for any given probability of sighting, the likely recapture profile of the recaptured animals. The predicted recapture profile is then compared with the actual profile and a sum of squares is calculated. The probability of sighting has been calculated by iteratively minimizing the sum of squares. Approximate confidence intervals have been estimated using the techniques outlined by Draper and Smith (1966). A listing of this program in Microsoft Basic can be found in Appendix 3.

4.2.5 Multiple Release–Single Recapture Study

The aim of the multiple release-single recapture study was to increase the number of animals released in order to extend and diversify the studies of growth, mortality and movement, and to derive estimates of total population size. For this purpose abalone were tagged at some distance from the transect during June–July 1986, October – November 1986 and March 1987 (Table 4.1). The location and numbers of abalone released are shown in Fig. 4.2. Through this process I tried to distribute tagged abalone as widely as possible within the research area and in a way that reflected the distribution of the abalone population within the area.

During these taggings, abalone were collected from around an anchored dive boat and returned to the boat for tagging by divers using hookah equipment. The abalone were tagged and measured in the boat before being returned to the bottom by divers. Length, tag number, the position of the tag and incidence of accidental wounding were noted. With the exception of the time taken to tag and measure each individual abalone, the abalone were held in the water at all times; no animals was exposed to the atmosphere for more than 5 min, and most for a considerably shorter period. Upon release, each abalone was held to the substratum until it gripped it. The position of the anchored boat was estimated by triangulation, using fixed buoys on the permanent transect and sightings made with a hand held prismatic compass. This was assumed to be the point of release for the tagged abalone.

4.2.6 Final Recapture

During July and August 1987 four commercial divers were used to make a final recapture of tagged abalone. This was conducted as a fishdown experiment which is described in Chapter 5 . The divers fished freely over the entire research area, using their normal diving procedure. The divers fished to a minimum size limit of 132 mm for the purpose of the fishdown experiment; however they were requested to retain tagged undersize abalone when they handled them incidentally.

The position of each diver was monitored and recorded at regular intervals by research personnel aboard each diver's vessel (see 5.2.1.a for a more complete description). Positions were fixed using hand held prismatic compasses to take sightings off two dan poles moored on the permanent transect. The research personnel also searched the catch for tagged abalone, recording in which bag of abalone each tagged abalone was found. Tagged abalone were identified as coming from a particular bag of abalone collected by an individual divers swimming a particular plotted path. The recapture site of each abalone was estimated as the point along a diver's path closest to where the abalone had been released.

All recaptured abalone were measured for length to the nearest millimetre. Growth increment data were analysed using the techniques described in Section 2.2.4.

4.2.7 Double Tagging Studies

Double tagging was conducted as a part of both facets of the tagging study. A total of 197 abalone were double tagged and released around the transect during the first period of tagging (February 1985). Animals from this release were available for recapture by research divers on five occasions prior to the final recapture.

Releases of double tagged abalone also occurred during each of the three periods of boat tagging with a total of 198, 258 and 221 double tagged abalone being released during June-July 1986, October-November 1986 and March 1987 respectively. Double tagged animals were distributed throughout the research site on these occasions.

With double tagged abalone the tags were attached as far from the growing margin as was practically possible. The respiratory pore to which each tag was attached to was noted.

The equation used to estimate tag losses was:

$$Pt_{,k} = n_{dsk} / (n_{dsk} + 2n_{ddk}) \quad \text{eq. 4.6}$$

where $Pt_{,k}$ is the probability of an abalone tagged during the k th time period losing a

tag before recapture; n_{ddk} is the number of abalone that were double tagged during the k th time period and recovered with both tags; and n_{dsk} is the number of animals doubled tagged during the k th time period and recovered with only one tag. This equation has been drawn from Chapman *et al.* (1965).

4.3 RESULTS

4.3.1 Supplementary Results

4.3.1.a Anaesthetic Sampling

A total of 42 x 1m² were sampled with the anaesthetic technique. The rock sheets and large boulders in the area made the area less suitable for sampling with this technique than the other study sites (v. Chapters 2 & 3), as little substratum material could be turned or brought to the surface. Because so little of the bottom could be sampled, the square used to delineate samples was not thrown randomly, and had to be placed on sites suitable for sampling. This undoubtedly biased any measurements of density. Despite this limitation, the length frequency histograms obtained with this technique are similar to those from other sites sampled with this technique (Fig. 4.5). The main features of the histogram are the youngest year classes and the accumulation of older emergent individuals at sizes >120 mm. The youngest year class was evident as a mode at 5-10 mm. Very few larger juveniles were taken in the samples. This probably reflects the size structure of the population, with the older year classes being numerically less abundant than the youngest animals (v. 2.4.5), but is also a measure of the inefficiency of the sampling technique on this type of bottom.

4.3.1.b Structure of the Emergent Population

A total of 111 emergent abalone were collected from the 15 x 15 m area searched in the *Durvillaea* habitat, of these 103 were >120 mm in length (Fig. 4.6a). A total of 88 legal sized (>131 mm) abalone were found in the 225 m² area, a density of 0.39 ab.m⁻². These emergent animals correspond to the relatively abundant group of larger animals which were a feature of the length-frequency histograms obtained using the anaesthetic technique. The non-cryptic animals ranged in age from 4-15 y-old with the most abundant age classes being 7-9 y-old (Fig. 4.6b). In this population the majority of abalone do not emerge from the sub-boulder habitat until 7 years of age or older. The effect of the three year closure to commercial fishing on the structure of the population is also evident with the three most recently recruited year classes being the most numerous animals in the

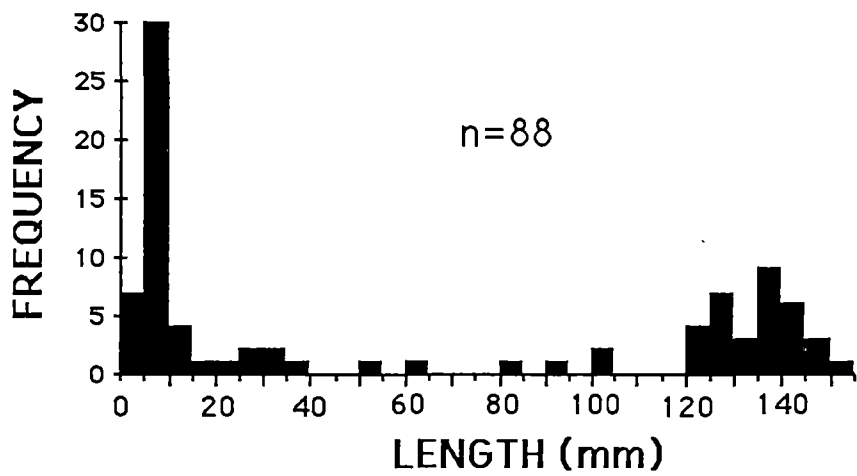


Figure 4.5
Length-frequency histogram of *Haliotis rubra* collected using the anaesthetic sampling technique at George III Rock.

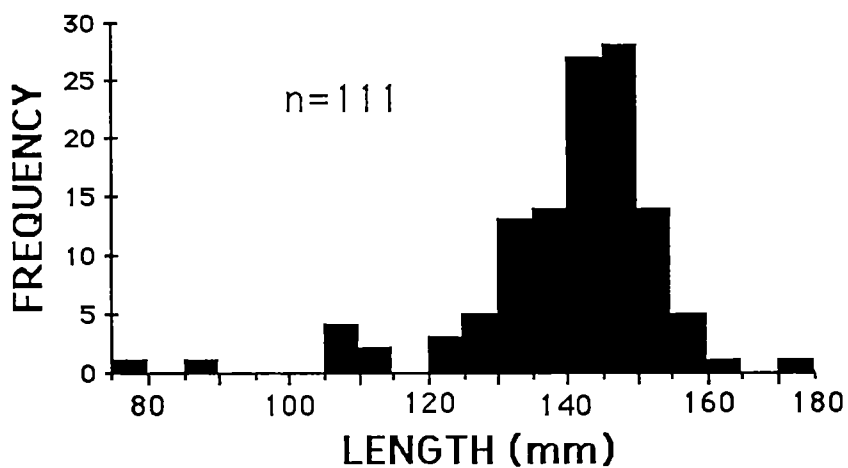


Figure 4.6a
Length-frequency histogram of emergent *Halotis rubra* collected by searching research divers at George III Rock.

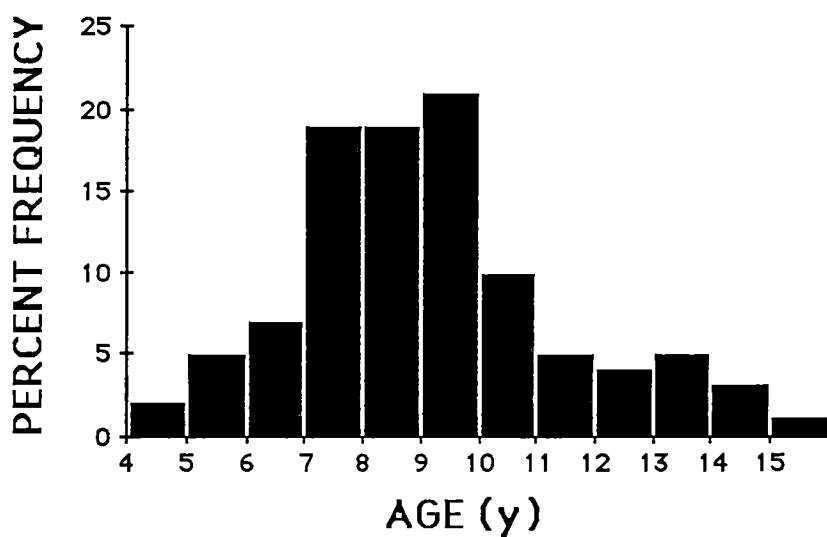


Figure 4.6b
Age-frequency histogram of emergent *Halotis rubra* collected by searching research divers at George III Rock.

population.

4.3.1.c Ageing and Growth

With the exception of the smallest size class of abalone found during the anaesthetic sampling (modal length of 5–10 mm), all the abalone taken in the different samples during June 1987 were aged. On the basis of the length frequency histograms and the Blubber Head study (v. 2.3.2.a) it has been assumed that this smallest class of abalone were spawned in October 1986, and they have been included in this analysis of growth as being 8 months old.

The growth curve indicated by direct ageing of animals was markedly sigmoid in shape (Fig. 4.7) and was not well described by a Von Bertalanffy equation. Consequently a Gompertz equation was fitted. This equation has the form:

$$L = W_0 \times e^{(G \times (1 - e^{(-gt)}))} \quad \text{eq. 4.7}$$

where L is length in mm and t is time in years (Ricker 1979). The parameters estimated for the equation were 1.621 (s.e.=0.501), 4.560 (s.e.=0.303) and 0.498 (s.e.=0.020) for W_0 , G and g respectively.

4.3.1.d Reproduction

The gonad index of abalone at the research site increases from 0 in abalone <110 mm, reaching maximal values of 6.25 - 6.98 in animals >145 mm (Fig. 4.8). This suggests that within the population, the onset of maturity occurs at about 5 years of age, but that many animals in the population do not mature until older than 8 years of age. Unfortunately I completed this aspect of the study before developing a technique for ageing abalone (Prince *et al.* 1988) so I was unable to determine the relationship between age and maturity with accuracy.

4.3.1.e Feeding

Analysis of the gut fullness index using analysis of variance showed that the index varied significantly between the major habitats (Table 4.3). In proportion to the weight of the foot muscles abalone from the *Macrocystis* habitat had the greatest weight of food in their stomachs, while those from the *Durvillaea* had the least (Fig. 4.9a).

By percentage occurrence fleshy, branching rhodophytes were the dominant group of food items in the stomach contents of abalone from each environment, comprising

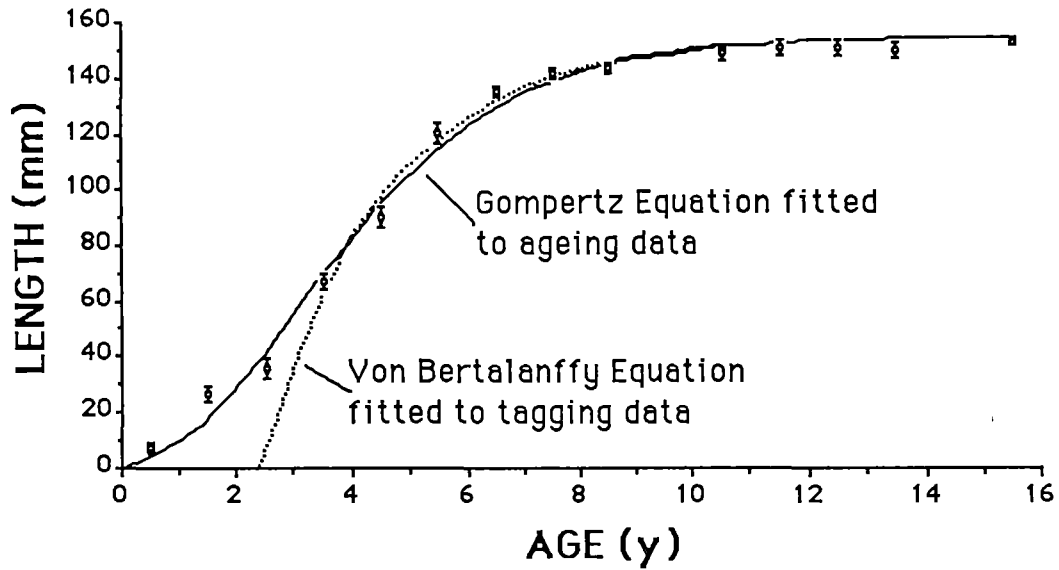


Figure 4.7

Growth curves estimated for *Haliotis rubra* at George III Rock. The Gompertz growth curve was fitted to the plotted length at age data, derived from direct ageing of shells, using the FISHPARM program of Prager *et al.* (1987); confidence intervals \pm s.e. The von Bertalanffy curve was fitted to tagging data using the method of Faben (1965) the t_0 has been estimated by minimizing the sum of the squared difference between the two curves.

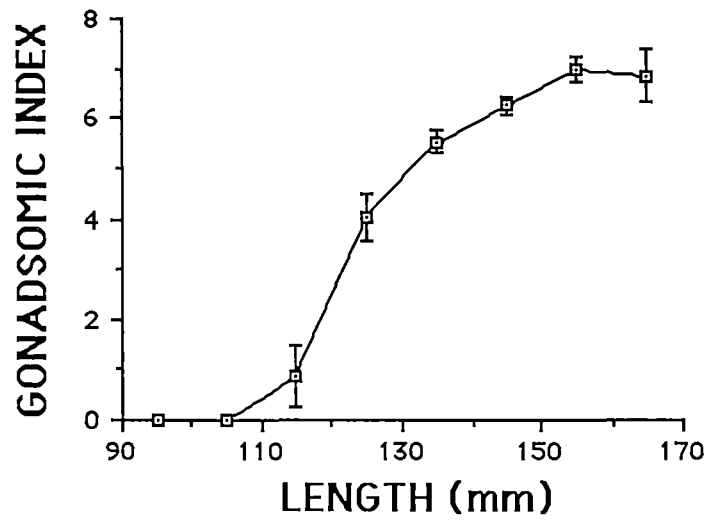


Figure 4.8
Relationship between size and gonad index (proportion of visceral mass cross section made up by gonad $\times 10$) of abalone collected during July 1987; bars indicate 95% confidence intervals (approximately 20 individuals per 10 mm length class).

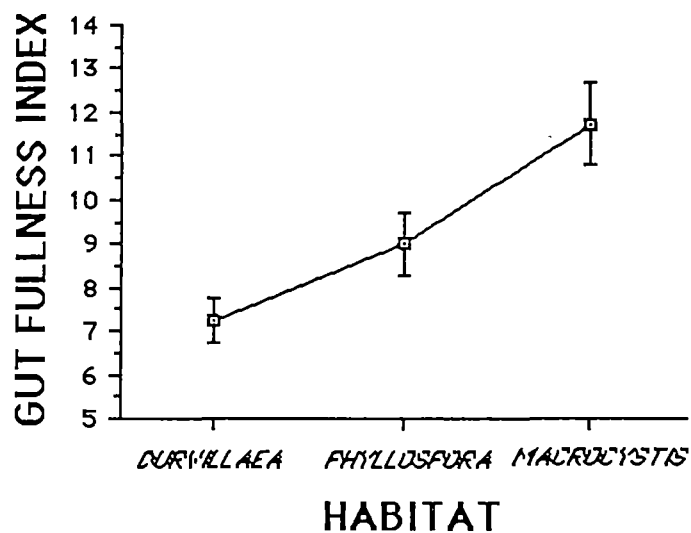


Figure 4.9a

Variation of the gut fullness index (weight of stomach contents as a percent of the weight of the foot muscle) between the three major habitats at George III Rock.

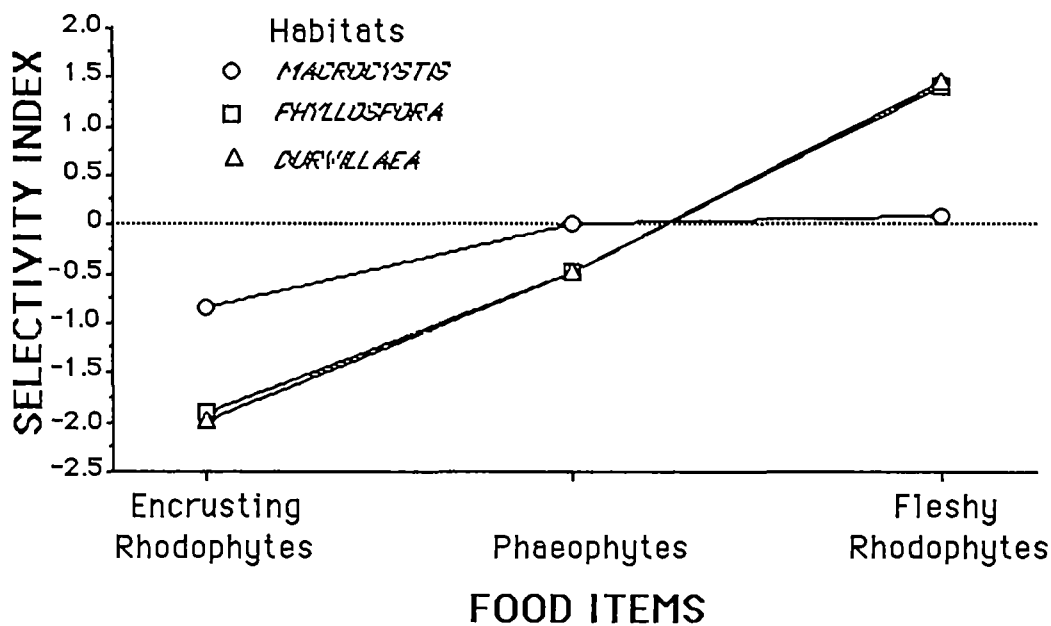


Figure 4.9b.

Variability in the selectivity index (log of the ratio of a food items occurrence in the gut to its occurrence in the environment) for phaeophytes, fleshy and encrusting rhodophytes between the three major habitats at George III Rock.

approximately 94, 50 and 58 % of the stomach contents in the *Macrocystis*, *Phyllospora* and *Durvillaea* habitats respectively. The abundance of these plants, expressed as percentage bottom cover was approximately 75, 2 and 2% for each habitat respectively (J.C. Sanderson, pers. comm.).

Table 4.3 ANOVA table for an analysis of variance comparing gut fullness indices (weight of stomach contents as a percent of foot weight) of abalone collected in the three major habitats at George III Rock.

Source	d.f.	Sum of squares	Mean Square	F-test	P
Between Groups	2	1678.4	839.2	40.05	0.0001
Within Groups	446	9344.9	20.9		
Total	448	11023.3			

The large phaeophytes, by occurrence, were the next most important food item making up approximately 5, 36 and 33 % of the food items in abalone from the respective habitats. In the *Macrocystis*, *Phyllospora* and *Durvillaea* habitats large phaeophytes covered approximately 5, 110 and 100% of the bottom respectively.

Encrusting animals were the next most important category of food items comprising 0.9, 13.7 and 8.3% of the food items in the respective habitats. This item of the diet is probably ingested incidentally as epiphytic organisms growing on macroalgae. As the relative importance of this item between the habitat seems to reflect the level of epiphytic growth observed on the macroalgae in each habitat.

Encrusting rhodophytes were not found to be an important food item and were only detected in samples from the *Phyllospora* habitat (0.2%). This was despite the fact that they are an important feature of each environment covering approximately 7, 80 and 95% of *Macrocystis*, *Phyllospora* and *Durvillaea* habitats.

Variation of the logarithmic selectivity indices (eq. 4.1) through the different environments are shown in Fig. 4.9b. These data show that abalone selected strongly for the fleshy rhodophytes in both the *Phyllospora* and *Durvillaea* habitats. In the *Macrocystis* habitat the selection for this food item was still positive but weaker, presumably because of the abundance of the food item in the habitat. The other major food items were not selected for in any habitat, with the strongest negative selectivity being displayed towards the encrusting corallines in each habitat.

In the *Macrocystis* habitat where the fleshy rhodophytes are abundant and the

phaeophytes relatively rare, both ingredients occurred in the diet of abalone in proportion to their abundance in the environment. This suggests that where sufficient of the required food item is available the abalone adopt a relatively passive mode of feeding.

4.3.2 Multiple Release-Recapture Results

4.3.2.a Movement

A total of 1 219 individual movements were observed between points on the permanent transect. It was evident, that compared to the area searched either side of the transect, movements were relatively extended. As this was likely to bias any estimates of movement no analysis has been performed on these data as a whole.

Figure 4.10 shows the movement of abalone recaptured or released in five haphazardly selected areas of the grid; some abalone moved relatively large distances in a short time span. The fastest recorded movement was approximately 40 m within a single night. There is some suggestion of directionality, with movements towards the shallowest part of the study site being favoured. Using the topography of the permanent transect to relate spatial position, to depth it was found that of the 1 219 individual movements observed, 35.5% were to shallower positions while only 16.6% were to deeper positions. In 47.9% of the moves the change in depth was minimal. A binomial test was used to test the hypothesis that if an abalone changed depth it was as probable, or more probable that it would move to a deeper rather than shallower position. This hypothesis was rejected ($z=9.126$, $p<0.001$) showing that the abalone were less likely to move towards deeper positions.

The orientation of the transect is such that movement towards shallower water from most parts of the transect coincides with movement into the predominantly south-south-east swell (Fig. 4.2). To distinguish movement towards the approaching swells from movement towards shallower water, I made a separate analysis of the movement patterns of abalone captured to the south of the shallowest region of the reef. A total of 246 release and recapture records were collected from this area of the transect; 78 movements were to shallower positions, 54 were to deeper positions and in 114 cases depth was not changed to any great extent. The hypothesis that if movement in relation to depth occurred it was as likely, or more likely, to be towards a greater depth than a shallower depth, was rejected ($z=2.10$, $p<0.05$).

4.3.2.b Multiple-Release-Recapture Parameter Estimation

Figure 4.11 shows the decline in recapture rate with time at liberty, for abalone released within the grid. This decline is attributable to movement, tag loss and mortality. These data are the pooled raw data on which the following analysis is based.

Table 4.4 shows the values fitted iteratively to the parameters by the population model. The model estimated that the probability of movement towards shallower depths in each month (0.076, 0.085 for South and East, respectively) was greater than towards greater depths (0.045 for both North and West). It should also be noted that because of the alignment of the grid none of the four cardinal directions represents movement directly towards shallower water. If movement directly towards shallower water is the greatest movement, and it is oblique to the grid's cardinal directions, the model is likely to underestimate the true rate of movement towards shallower depths.

The sum of squares value (1014.1) was reduced to 701.3 when a simple spatial structure was added to the model's description of movement. In this modified version each of the 5 east-west rows of cells (Fig. 4.4) have been given a movement index which weighted the proportion of abalone moving East, West, North and South from or within that row:

$$N_{dir.} = (N_t \times Mov_{dir.}) \times MovIndex_r \quad \text{eq. 4.8}$$

where $MovIndex_r$ is the movement index for the r-th row of grid cells. For each row of cells (North to South) the values fitted to $MovIndex_r$ by minimizing the sum of squares were 0.1, 0.5, 1.4, 1.8, 1.6 respectively. These values basically follow the 9 m depth contour (Fig. 4.4), which also marked a change in habitat, with those above the 9 m contour having a higher value than those below. These results suggest a greater degree of movement above the 9 m depth contour, that is, in the *Durvillaea* habitat.

The negative value for initial tag loss and tagging mortality derived by the model appears anomalous. This value suggests that 25% more abalone existed immediately after release than were actually released. The most plausible explanation for this is that the probability of recapture is not constant over time. If newly released abalone have a higher probability of being sighted than abalone at liberty for longer periods the iterative multiple-release-recapture model may attempt to fit this by varying the initial tagging loss.

A clear mechanism for non-constant catchability does exist. Emergent abalone are generally heavily covered in marine growth which effectively camouflages them making it difficult for divers to find them. It was observed that newly applied tags disrupted this camouflage and, until they became overgrown with marine growth, increased the ability

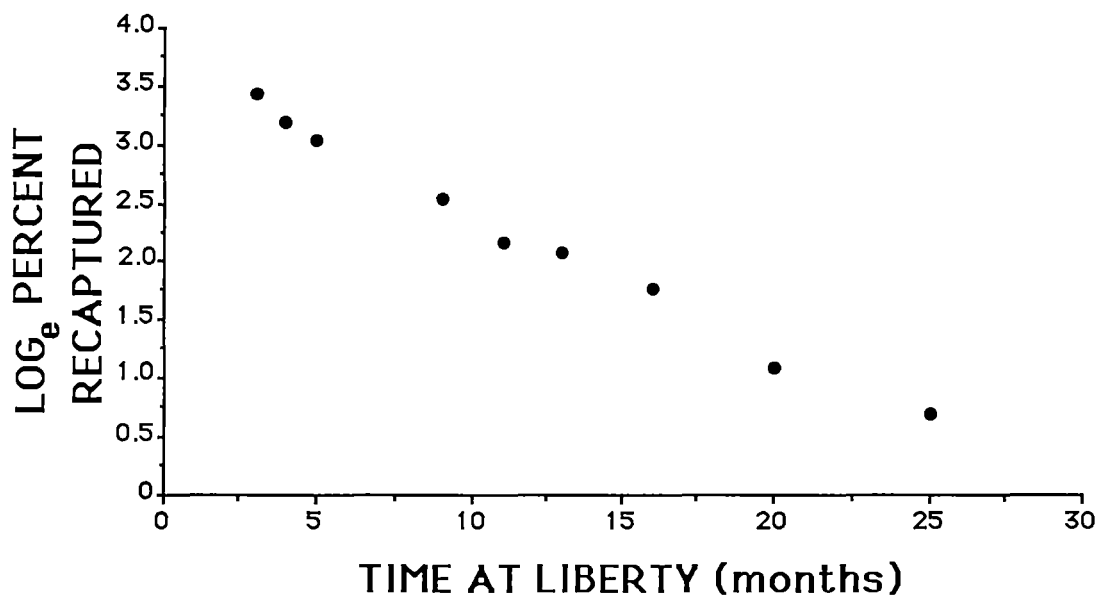


Figure 4.11
Recapture rate (percent of releases \log_e converted) of abalone released and recaptured within the permanent grid, plotted against time at liberty.

of research divers to detect them. The growth of marine organisms on the tags was observed to be relatively rapid. This suggests that the probability of sighting would be more accurately modeled by a variable which declines with time towards some constant.

Table 4.4 Parameter values estimated by the first (a) and final (b) versions of the iterative multiple-release-recapture model when all values were estimated iteratively.

Parameter	Estimated Value (a)	Estimated Value (b)
Initial tag loss & tagging mortality	-0.25 release ⁻¹	-0.04 release ⁻¹
Continuing tag loss & natural mortality	0.063 month ⁻¹	0.062 month ⁻¹
Sighting probability	0.346 recapture ⁻¹	-
Movement North	0.045 month ⁻¹	0.038 month ⁻¹
Movement South	0.076 month ⁻¹	0.104 month ⁻¹
Movement West	0.045 month ⁻¹	0.060 month ⁻¹
Movement East	0.085 month ⁻¹	0.091 month ⁻¹
Asymptotic probability of sighting	-	0.485 recapture ⁻¹
Sighting Constant K	-	0.35
Sighting Constant B	-	6.50
Movement Index Row 1	-	0.1
Movement Index Row 2	-	0.5
Movement Index Row 3	-	1.4
Movement Index Row 4	-	1.8
Movement Index Row 5	-	1.6
Number of observations	1296	1296
Sum of squares	1014.1	678.8

Accordingly I modified the model so that the probability of sighting an abalone during any search was determined by the time it had been at liberty. Initially a three parameter equation was used:

$$\text{Obs}N_t = N_t \times \text{ProbObs} \times (1+(K/T)) \qquad \text{eq. 4.9}$$

where ProbObs is the asymptotic value which the probability of sighting approaches, K is a constant and T is time at liberty measured in months. However when this parameter was used the model converged on values which retained the characteristics of constant catchability.

Subsequently a four parameter equation was used:

$$\text{Obs}N_t = N_t \times \text{ProbObs} \times (1+(B \times e^{-T/K})) \qquad \text{eq. 4.10}$$

where ProbObs is the asymptotic value which the probability of sighting approaches, K and B are constants and T is time at liberty measured in months. This was only marginally successful, reducing the sum of squares value from 701.3 to 678.8 and increasing the estimated initial loss and mortality value from -0.25 to -0.04, which within the error structure of these estimates is indistinguishable from a zero value. However the modified version of the model increased the estimated probability of sighting abalone, from 0.346 to 0.485 and increased the estimated rates of movement, suggesting that animals had a higher probability of recapture but were less likely to remain within the area.

The estimated parameters describing the variability of catchability suggest that during the first month after release the probability of recapture was approximately 37% greater than the asymptotic value. The probability of recapture however approaches the asymptotic value extremely rapidly being within 0.1% of the asymptote after 3 months at liberty. These parameters imply that the model has an unreal level of resolution and as the minimum time between release and recapture was 3 months the model is effectively using a constant probability of sighting to fit the data.

4.3.2.c Independent Estimation of the Probability of Recapture

To resolve this situation I decided to use additional information contained within the data set to independently estimate the probability of a tagged abalone being observed during a search. To do this I made a second iterative model which used the recapture histories of abalone released during the first and third recapture/searches and recaptured at least two recapture/searches later. I assumed that these abalone were available within the grid for recapture up until their final recapture i.e. they had not moved out of the grid and then returned. This allowed the probability of recapture to be estimated iteratively. The multiple-release-recapture model does not use any information regarding the recapture histories of the abalone so this latter data set can be regarded as independent of the former data set. The data used for this analysis are contained in Table 4.5.

The lowest sum of squares (127.0) for the 36 observations was obtained with a sighting probability of 0.32 and this value had an approximate 95% confidence interval of 0.25-0.39.

The weakness of the version of the model contained in Appendix 3 is that each recapture event contributes to the sum of squares in proportion to the square of the number of animals recaptured. If the size of the recaptures were to vary considerably, disproportionate weight might be given, when the sum of squares was minimized, to a

small number of large recaptures. This particular data set appears to be relatively robust to this type of bias because when the model was modified to weight all recapture events evenly, a value of 0.33 was estimated for the probability of recapture.

Table 4.5 Recapture data used to estimate the probability of recapturing tagged abalone within the grid.

	Recaptures					
	2nd	3rd	4th	5th	6th	n
<hr/>						
First Release						
	*	*	*	*	*	1
Recaptured	*	*			*	2
Sixth Search			*	*	*	1
	*				*	1
					*	3
<hr/>						
Recaptured	*	*	*	*		1
Fifth Search		*	*	*		2
	*	*		*		1
		*		*		1
				*		4
<hr/>						
Recaptured	*	*	*			3
Fourth Search		*	*			5
	*		*			9
			*			12
<hr/>						
Recaptured	*	*				9
Third Search		*				34
<hr/>						
Third Release						
Recaptured Sixth Search			*	*	*	4
			*	*		3
			*		*	8
					*	9
<hr/>						
Recaptured Fifth Search			*	*		14
				*		16
<hr/>						

These estimates approximate the value derived above by the first version of the multiple-release-recapture model for the probability of sighting. I modified this program to describe sighting probability with both of the more complex forms of sighting probability (eq. 4.9 & 4.10). However when the model was allowed to iterate and fit its

own values to these variables the model moved the values for K and B towards values that effectively described sighting probability with a constant value of 0.32. Constraining the model to take the values derived from the multiple-release-recapture model increased the sum of squares value considerably, from 127.0 to >350.

4.3.2.d *Final Parameter Estimates of the Multiple-Release-Recapture Model*

Using this independent estimate of sighting probability I re-analysed the multiple-release-recapture data. For this final analysis I described the probability of recapture with the four parameter model (eq. 4.10) and fixed the asymptotic probability of sighting at 0.32. Because the sighting probability was fixed at a value similar to that derived initially, the model still tended to towards the previously derived negative value for the initial loss and mortality (-0.25). However, because it is impossible for the proportion of initial losses to be a negative value, I constrained the model to use a value of zero for this parameter. This forced the model to describe this feature of the data purely in terms of the parameters provided.

When constrained to use these values, the iterations converged at a sum of squares value of 737.2 somewhat above the minimum of 678.8 observed with the penultimate model. The parameters describing the probability of sighting and on which the model converged (Table 4.6) suggest that 3 months after release abalone are still 21% more likely to be sighted than they are in the long term; however the probability of sighting declines to the asymptotic value after 8 months at liberty. These values are consistent with qualitative impressions gathered during the experiment and with the visual appearance of the raw data presented in Fig. 4.11.

The final estimates of the movement parameters were similar to the preliminary estimates, however the final estimate of continuing loss through mortality and tag shedding (0.035) is considerably lower than the preliminary estimates. Joint confidence intervals (Fig. 4.12a-c) show that there is considerable interaction between the parameters describing sighting probability, mortality and tag loss, and initial losses. It can also be seen that constraining the model with regard to initial losses forced the model towards lower estimates of mortality and tag loss (Fig. 4.12c). Obviously inaccuracies in the equation used to describe sighting probability or in the estimate of sighting probability will bias this estimate of mortality and tag loss.

Figure 4.12

Joint confidence intervals for selected parameters estimated using the iterative multiple-release-recapture model; a. Sighting constant (k) and monthly rate of mortality and tag loss. b. Initial loss and probability of recapture. c. Initial loss and monthly rate of mortality and tag loss.

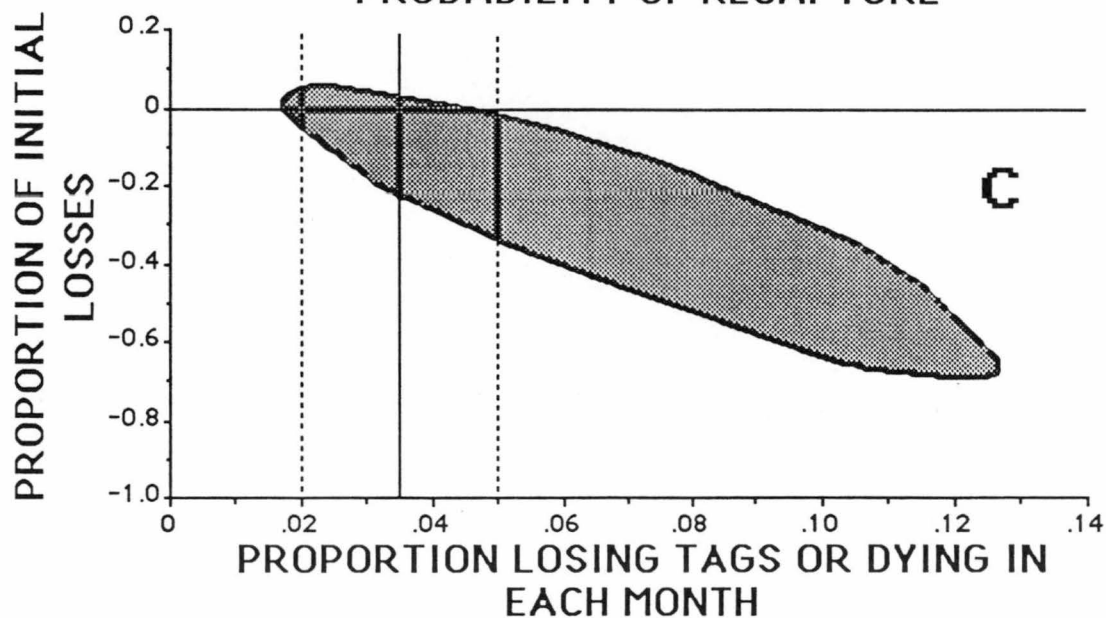
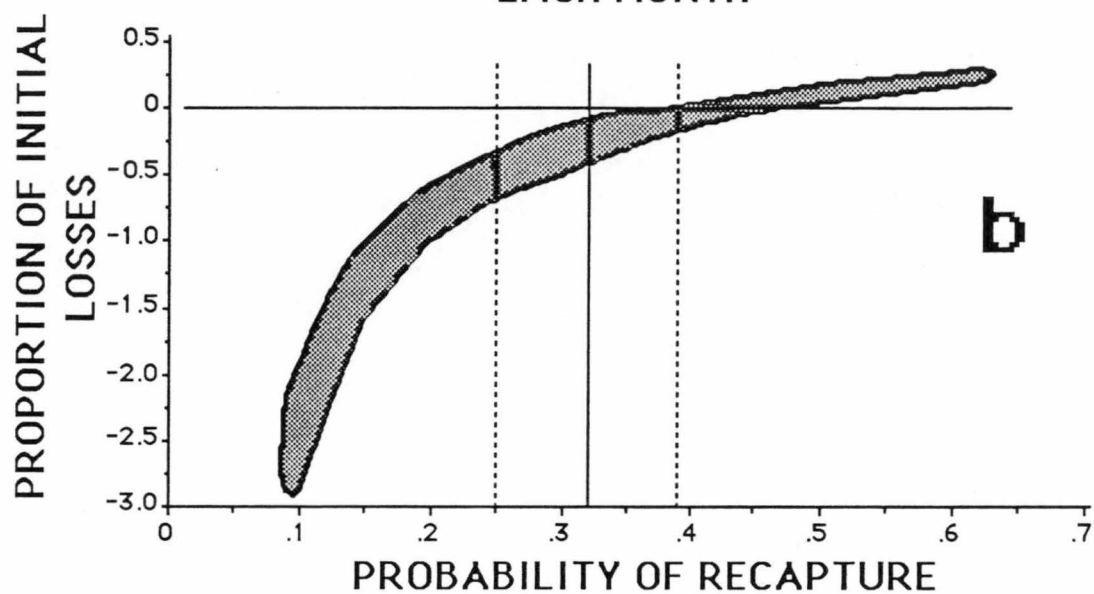
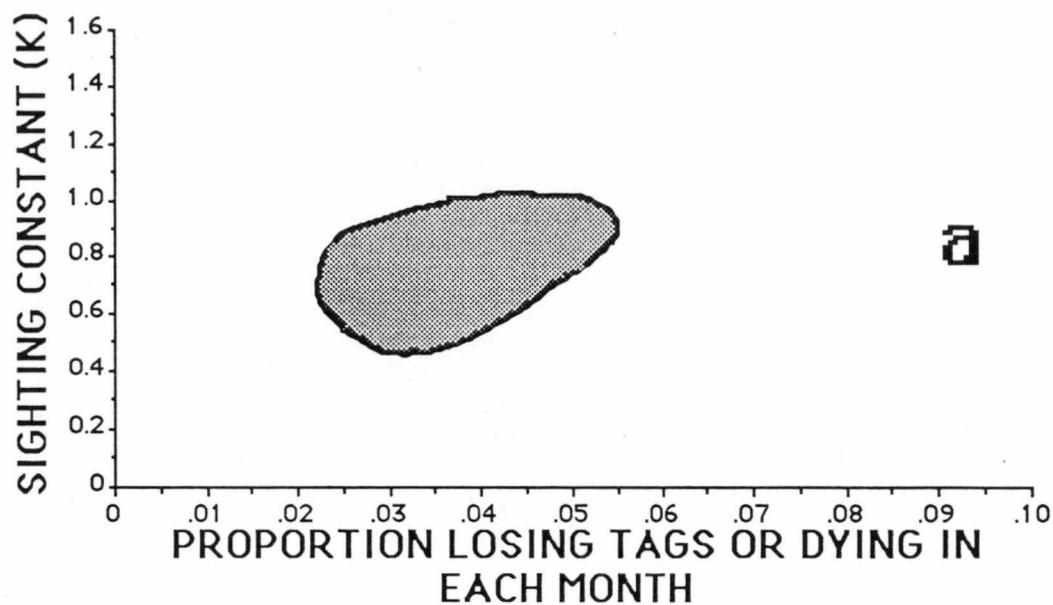


Table 4.6 Final estimates of the parameters of the iterative multiple-release-recapture model, together with 95% confidence limits.

Parameter	Estimated Value	95% Confidence Int.
Initial tag loss & tagging mortality	0	Fixed
Continuing tag loss & natural mortality	0.035 month ⁻¹	0.02 - 0.05
Movement North	0.03 month ⁻¹	0.015 - 0.045
Movement South	0.08 month ⁻¹	0.060 - 0.100
Movement West	0.04 month ⁻¹	0.015 - 0.065
Movement East	0.08 month ⁻¹	0.050 - 0.095
Asymptotic probability of sighting	0.32 recapture ⁻¹	Fixed
Sighting Constant K	0.8	0.5 - 1.1
Sighting Constant B	9.0	2.0 - 15.0
Movement Index Row 1	0.1	-0.6 - 1.3
Movement Index Row 2	0.5	0.4 - 0.6
Movement Index Row 3	1.4	1.1 - 1.8
Movement Index Row 4	1.8	1.4 - 2.2
Movement Index Row 5	1.6	-0.4 - 6.8
Number of observations	1296	
Sum of squares	737.2	

4.3.2.e Double Tagging Results

Double tagged abalone released in February-March 1985 were recaptured on six occasions, including the final fishdown event (Table 4.7). It should be noted that while the majority of these double tagged abalone were released within the grid system, these data include releases made over the entire transect and recaptures made throughout the research site. The proportion of tags estimated to have been shed after 3, 9, 13, 20, 25 and 28 months at liberty respectively, were 0.164, 0.278, 0.310, 0.250, 0.333 and 0.500. When the proportion of tags retained were log_e transformed and regressed against time at liberty, the relationship:

$$\text{Proportion Retained} = e^{(-0.17 \times (\text{years at liberty})) - 0.15}$$

was found to be significant (r²=0.62, n=6, p=0.06).

4.3.3 Multiple Release - Single Recapture Results

4.3.3.a Double Tagging Results

More double tag data were generated through the releases of double tagged abalone

that occurred during June-July 1986, October-November 1986 and March 1987 (Table 4.7).

When all these double tag data were combined the relationship between tag loss and time at liberty:

$$\text{Proportion Retained} = e^{(-0.15 \times (\text{years at liberty}))} - 0.17$$

was found to be significant ($r^2=0.53$, $n=9$, $p<0.05$). These relationships indicate an initial tag loss of 17-19% and a continuing annual tag loss of approximately 14%.

Table 4.7 Summarized recapture data for double tagged abalone.

Release Date	Number Released	Recapture Date	Months at Liberty	Lost Tag 1	Lost Tag 2	Both Tags Intact	Proportion Retained
Feb. 1985	197	May 1985	3	1	19	51	0.84
		Nov. 1985	9	6	4	13	0.72
		Mar. 1985	13	1	8	10	0.69
		Oct. 1986	20	1	3	6	0.75
		Mar. 1987	25	1	13	4	0.67
		Jul. 1987	28	3	13	8	0.50
June 1986	198	Jul. 1987	13	3	13	8	0.82
Oct. 1986	258	Jul. 1987	9	11	10	24	0.69
Mar. 1987	221	Jul. 1987	4	18	26	71	0.76

4.3.3.b Growth

The data used in this analysis were the size increment data for abalone released throughout the course of the tagging program, and which were recaptured in July 1987. To reduce the effect of seasonality and errors of measurement only recaptures with a time at liberty of ≥ 12 months were used in this analysis of growth. At the time of release the mean size of the 662 abalone used in this analysis was 134 mm (s.e.=0.514), sizes ranged from 89-166 mm. At the time of recapture the mean size of the recaptured animals was 144 mm (s.e.=0.338) and the range was 117-176 mm.

When all the recaptures were pooled the asymptotic length of the population, L_{∞} , and the growth coefficient, K , were estimated at 154.7 mm (s.e.=0.72) and 0.471 (s.e.=0.021) respectively, when time is in years. The 134 animals released and recaptured in the *Macrocystis* habitat were analysed separately to the 528 abalone in the *Durvillaea* habitat. The growth parameter L_{∞} was estimated as 154.4 mm (s.e.=1.85) and 154.7

(s.e.=0.78) respectively; while K was estimated at 0.418 (s.e.=0.046) and 0.483 (s.e.=0.0234). The hypothesis that these values were unequal was tested and rejected ($t=0.13$, d.f.=660, $p>0.10$; $t=0.80$, d.f.=660, $p>0.10$ respectively).

When the difference between the von Bertalanffy curve derived from tagging and Gompertz equation derived from the length at age data, is minimized using a least squares routine, a t_0 of 2.4 y is suggested for use with the former equation (Fig. 4.7).

4.3.3.c Movement

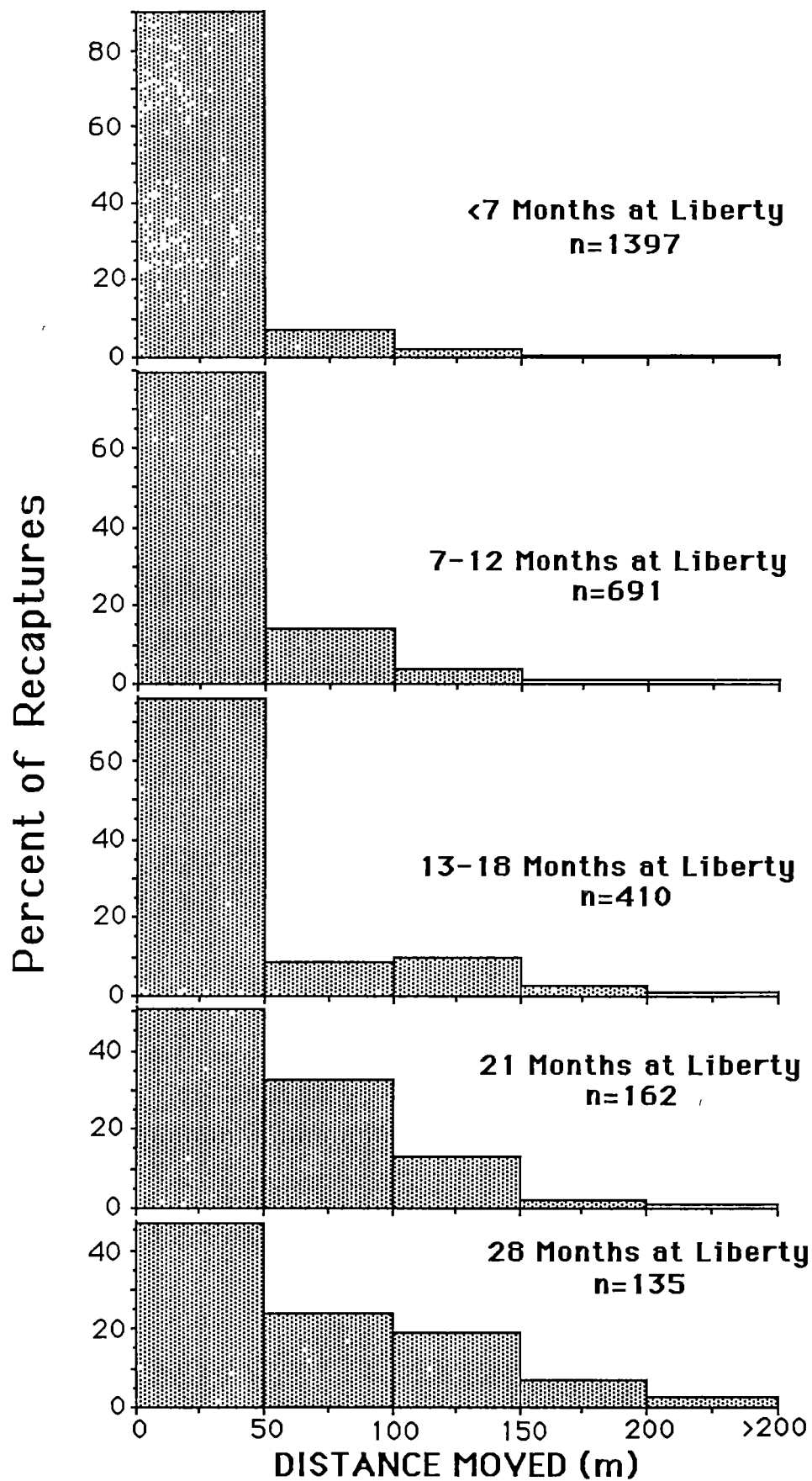
The movement data presented below have been drawn from the releases made throughout the tagging study and recaptured in July 1987 as a part of the fishdown experiment. Assuming that abalone did not move out of the research site these data can be expected to provide relatively unbiased estimates of distances moved because the entire research site was fished during the recapture period. However the site of recapture for these records was necessarily imprecise because of the methodology of the fishdown experiment. From practical experience during the study an error of ± 50 m is suggested for these estimates of distance moved.

The data show that abalone generally did not move long distances. Overall 80% of the recaptured abalone moved less than 50 m from the point at which they were released (Fig. 4.13). The proportion remaining within 50 m of the release point decreased as time at liberty increased, showing that movement over time was occurring and that the movement observed was not caused solely by handling during tagging. Some reasonably large movements over time were observed with 10% of the abalone at liberty for more than 18 months moving at least 150 m.

The movement patterns of abalone tagged in the two different dominant habitats show that less movement occurred in the *Macrocystis* habitat (Fig. 4.14). In both habitats the estimated rate of movement (total distance moved per month at liberty) decreased with time. In the *Macrocystis* habitat the average rate of movement for an abalone at liberty for 4 months was 3.5 m.month^{-1} (s.e.=0.16) for those at liberty 28 months this declined to $1.26 \text{ m.month}^{-1}$ (s.e.=0.52), in the *Durvillaea* habitat these figures were $7.81 \text{ m.month}^{-1}$ (s.e.=0.34) and $2.80 \text{ m.month}^{-1}$ (s.e.=0.25) respectively. Errors associated with accurately determining the points of release and recapture can undoubtedly be expected to contribute to this decline in the movement rate with time at liberty. This is because over shorter release periods the error in measurement would be averaged over fewer months. However the trend probably also indicates that movements are relatively random and

Figure 4.13

Distance-moved-frequency histograms for abalone recaptured after <7, 7–12, 13–18, 21 and 28 months at liberty.



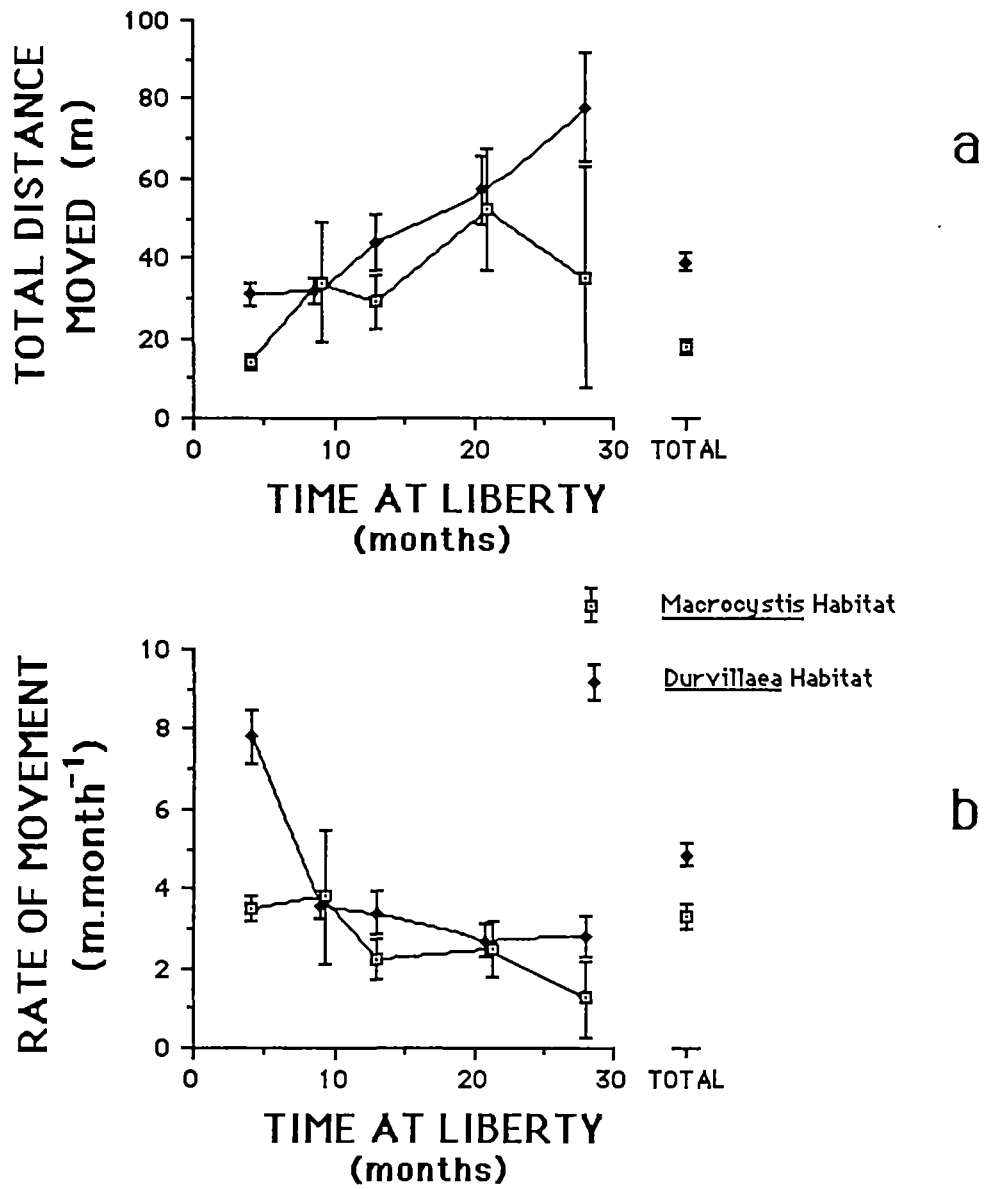


Figure 4.14
The relationship between total distance (a) or monthly rate of movement (b) and time at liberty in the two major habitats at George III Rock. Error bars indicate $\pm 95\%$ confidence intervals.

without specific direction. The average monthly movement for abalone at liberty in the *Macrocystis* habitat for ≥ 9 months was $2.59 \text{ m.month}^{-1}$ (s.e.=0.27) and $4.04 \text{ m month}^{-1}$ (s.e.=0.12) in the *Durvillaea*. While this trend towards greater rates of movement in the *Durvillaea* was consistent, it was not found to be significant ($t=1.39$, d.f.=1167, $p>0.05$).

The distance moved and the size of abalone was also examined (Fig. 4.15). In the *Durvillaea* habitat abalone at liberty for ≥ 9 months and recaptured when ≤ 135 mm were found to have moved an average distance of 29.1 m (s.e.=3.5), abalone 136–145 mm moved 39.4 m (s.e.=3.3) and abalone >145 mm moved 43.3 m (s.e.=2.0). The difference between the mean distance moved by the largest size group and the smallest size group was found to be highly significant ($t=3.69$, d.f.=1049, $p<0.001$). In the *Macrocystis* habitat the same trend was evident although less significant ($t=0.94$, d.f.=664, $p>0.10$), with the distances moved for each size class being 17.9 (s.e.=1.8), 19.1 (s.e.=1.5) and 20.4 (s.e.=1.65) respectively. The difference in mean distance moved by the largest size group of abalone released in each of the two habitats was found to be highly significant ($t=7.9$, d.f.=1188, $p<0.001$) with the movement in the *Durvillaea* habitat being greatest.

The direction of the 11 largest movements is shown in Fig. 4.16. No obvious pattern is apparent in these movements, although it should be noted that some movement occurred between the major habitat types. Most of these large movements started in the *Durvillaea* habitat which might have been expected as this is the habitat in which abalone are most mobile. However results here may be biased as the greatest number of animals were released into this habitat (Fig. 4.2).

In the context of these results an interesting phenomenon was noted. All the tagged abalone included in the above analysis were released within 20–30 m of the point at which they were captured. However between October and November, 1986 a single group of animals were captured within the *Durvillaea* habitat and released approximately 350 m away within the *Macrocystis* habitat (Fig. 4.17). This was because the latter area had few abalone naturally occurring in it and at the time I was interested in dispersing tagged abalone throughout the research site. Thirty two abalone recaptured from this release moved an average of 65.0 m (s.e.=16.6), while other abalone released at the same time in the *Macrocystis* habitats moved an average of 34.1 m (s.e.=7.8); those released in the *Durvillaea* habitat at the same time moved 32.1 m (s.e.=1.53). The hypothesis that the average distance moved by this relocated group was less than or equal to that of the other

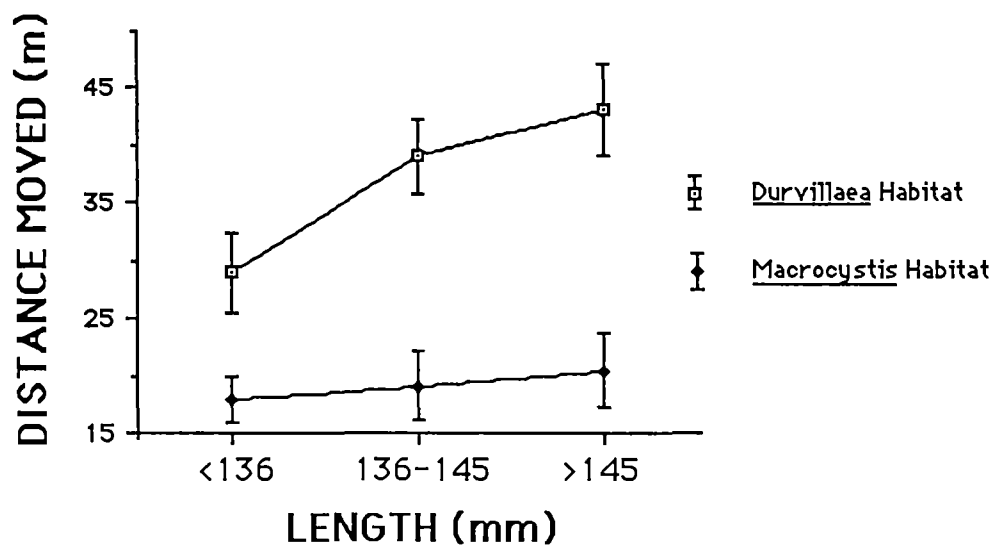


Figure 4.15
The variation in distance moved with size (maximum shell length mm) and habitat. Error bars indicate $\pm 95\%$ confidence intervals.

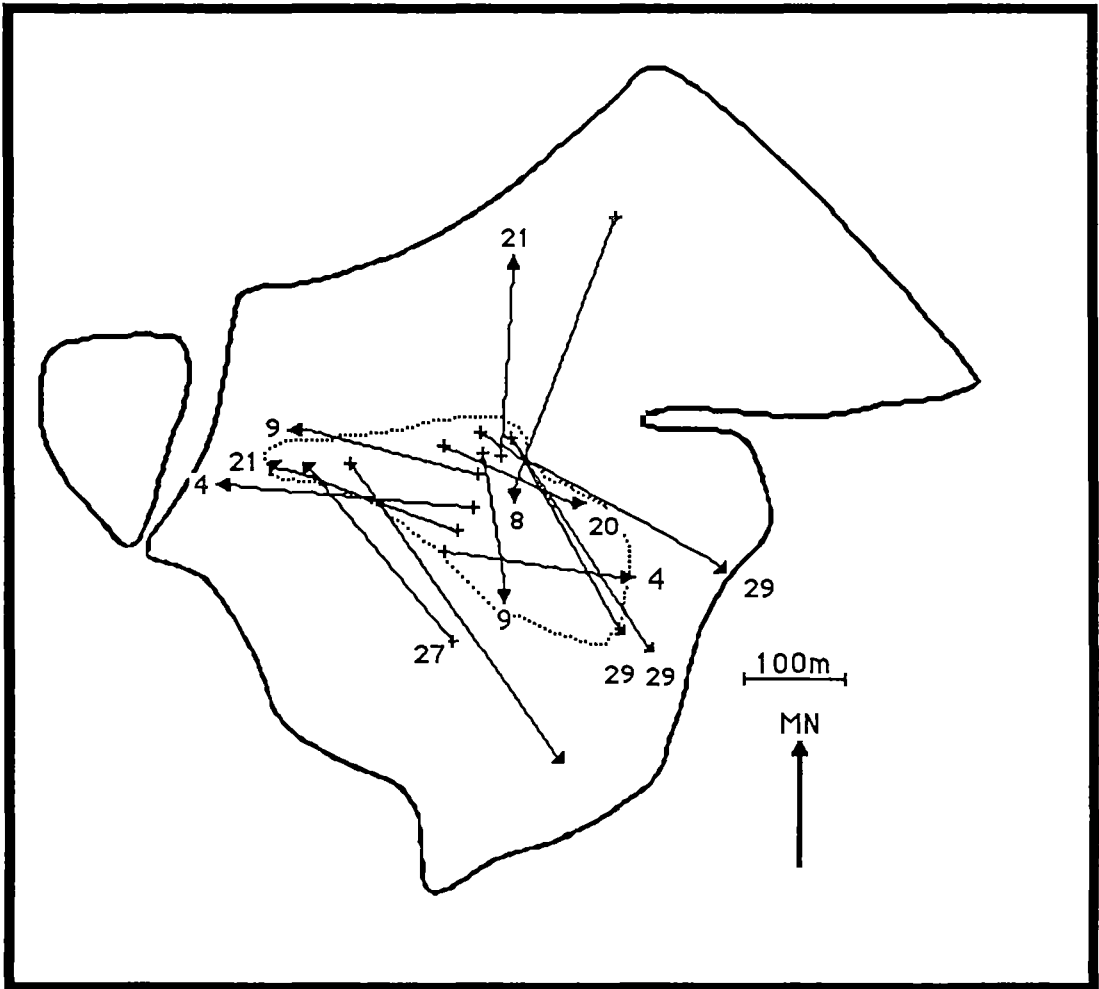


Figure 4.16
The direction of the 11 largest movements recorded for *Haliotis rubra* at George III Rock.

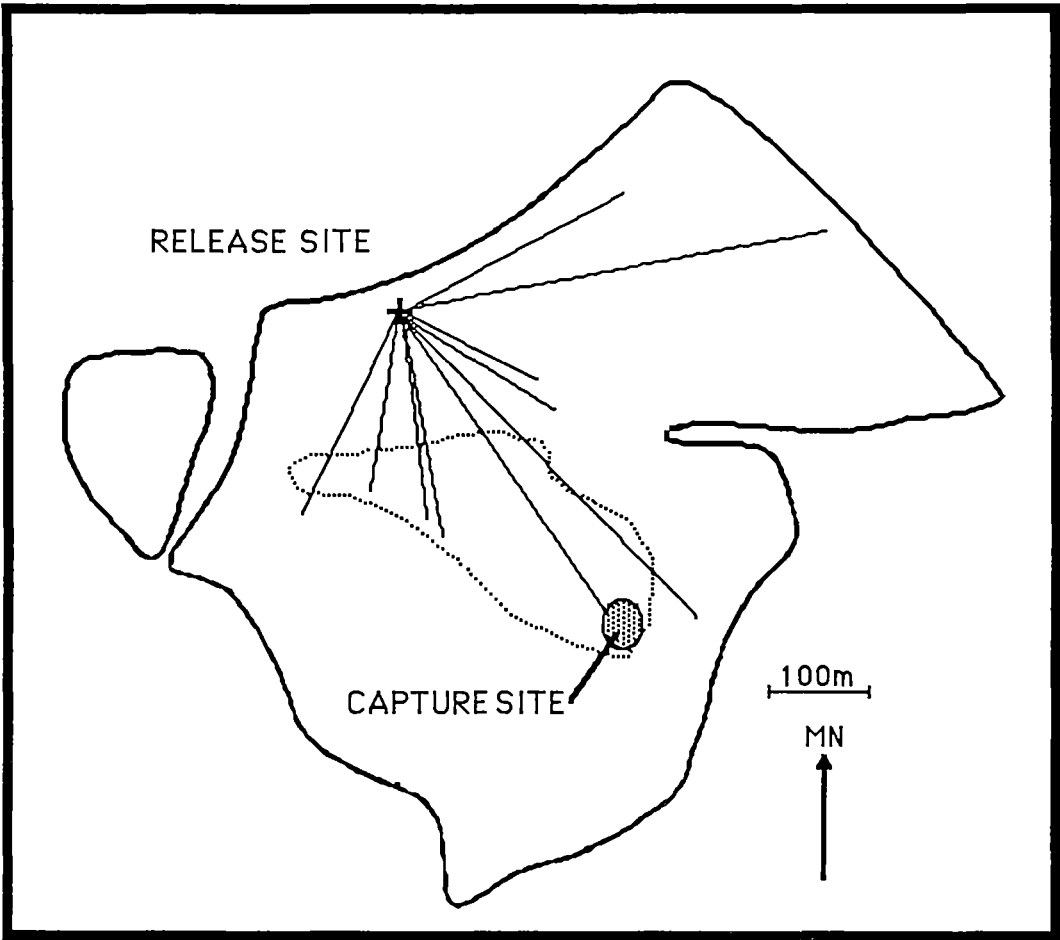


Figure 4.17
The anomalous movements displayed by *Halotis rubra* recaptured after initial capture in the *Durvillaea* habitat and release in the *Macrocystis* habitat.

two groups was tested with a one tailed unpaired t-test and rejected in both cases relocated releases vs. other *Macrocystis* habitat releases; d.f.=84, t=1.91, p<0.05; relocated releases vs. *Durvillaea* habitat releases; d.f.=635, t=4.29, p<0.001). The differing scales of movement is illustrated by the fact that 30% (10) of these relocated animals that were subsequently recaptured moved >50 m while only 6% of the other abalone released at this time moved equivalent distances.

Furthermore, 7 of the 10 abalone which had moved > 50 m, had moved towards their original capture site. Four of these 7 were in fact recaptured closer to their original capture site than to their release site (Fig. 4.17). The straight line path of movement for 6 of these 10 abalone was within 30° of a direct line between the capture and release sites. These observations indicate that these abalone may exhibit some form of directional movement towards the site at which they were captured.

Because the movement patterns of the abalone from this release were clearly anomalous they were excluded from the general analysis of movement.

4.3.3.d Tag Returns

The five major releases of tagged abalone occurred 28, 21, 13, 9 and 4 months prior to the final recapture. Using the von Bertalanffy growth parameters it can be estimated that for tagged abalone to have attained the legal minimum size of 132 mm by the time of the recapture they had to be at least 86.5, 102.9, 116.8, 122.4 and 128.1 mm in length at the time of each respective release. A total of 991, 819, 1 259, 1 417 and 3 051 abalone above these cut-off points were released during each respective period of tagging. From the respective periods of tagging 13.4, 18.9, 28.8, 43.8 and 40.4% of the animals expected to have attained legal size were recaptured. When the proportion recaptured from each tagging episode, \log_e converted is regressed against months at liberty a significant relationship is observed ($r^2=0.941$, $n=5$, $p<0.01$). This relationship can be expressed as:

$$\text{Proportion Recovered} = e^{(-0.614 \times (\text{years at liberty}))} - 0.564$$

This suggests an annual instantaneous rate of decline in abundance due to tag loss and mortality of 0.614 which is equivalent to an annual survival of approximately 54%. The results also suggest that the recapture rate of animals at liberty for zero years would have been 57%.

The above analysis assumes that all of the tagged abalone were equally vulnerable to being recaptured by divers, an assumption which is probably not valid in the light of the

results suggesting that recapture rates are related to the time at liberty. If the proportions recaptured are corrected using the sighting probability parameters derived from the multiple release recapture study (v. 4.3.2.d) the significant relationship:

$$\text{Corrected Proportion Recovered} = e^{(-0.602 \times (\text{years at liberty}))} - 0.592$$

is observed ($r^2=0.920$, $n=5$, $p<0.01$). This relationship implies an instantaneous annual rate of decline of 0.602 or 55% survival between years, and a probability of recapture, if time at liberty equals zero, of 55%.

4.4 DISCUSSION

4.4.1 Tagging

4.4.1.a Initial Tag Loss

The results of the double tagging study suggest an initial tag loss of approximately 17–19% which is in contrast to the iterative estimates of the multiple-release-recapture model which detected no initial loss. It is possible that this contrast is due to the model being incapable of resolving the effects of initial tag loss and mortality from that of other parameters such as the probability of sighting. From the joint confidence intervals of the asymptotic sighting probability and the initial losses parameter (Fig. 4.12b) it can be seen that these two variables are strongly and positively correlated, with high values of both being equally as probable as low values of both. The probability of sighting was estimated independently and fixed at 0.32. From the joint confidence intervals it is apparent that if this latter estimate were an underestimate a positive value for initial losses might possibly be obscured. However, even when the model was allowed to converge on a sighting probability of 0.485, the model still converged on a negative estimate for initial losses. This tendency towards a negative value for initial loss suggests that newly released abalone are more vulnerable to recapture than expected, presumably because the final description of sighting probability is inadequate. However the implication of this negative value is that any initial losses are small enough to be completely masked by the effect which causes newly released abalone to be more easily recaptured than expected. This would seem to argue that the magnitude of initial losses is relatively minor.

A second alternative for explaining the apparent contrast between the double tagging results and the multiple-release-recapture analysis could be the limitations of the double tagging experiment. The loss of second tags from double tagged abalone was observed to exceed the loss of first tags in 7 of the 9 recaptures (Table 4.7). The greatest difference (1 first tag:19 second tags) being observed amongst the double tagged abalone released in

February 1985 and recaptured 3 months later. This suggests that the position of the tag in the shell possibly effects the probability of initial tag loss. The first tag was placed, whenever possible, in the respiratory pore furthest from the growing margin, as were single tags. The second tag was placed in a respiratory pore closer to the growing edge.

The respiratory pore furthest from the growing margin is always the next functioning respiratory pore to be sealed with nacre as the abalone grows. A build-up of nacre was usually observed within this respiratory pore at the time of tagging, sometimes almost sealing the respiratory pore. This build-up of nacre made the conical respiratory pore less fragile and, consequently, less prone to cracking when the rivet attaching the tag expanded inside the pore. It was this observation made at the outset of the tagging program, and the expectation that less tags would be lost from this respiratory pore, which led to the decision to use this respiratory pore and to record to which respiratory pore the tags were attached.

In excess of 76% of the animals released within the grid were tagged in the respiratory pore furthest from the growing margin. Accepting that the initial tag loss when tags are applied to this respiratory pore could have been up to 19 times lower than the 17–19% observed when the tag is applied to other respiratory pores, and that 76% of the animals released were tagged in the first respiratory pore, a mean initial tag loss as low as 5% could have been possible during the normal tagging process. An initial tag loss of this magnitude would be consistent with the small loss suggested by the multiple-release-recapture model.

4.4.1.b *Tagging Mortality*

The negative estimates for initial losses imply that the underwater tagging process caused little if any mortality of abalone. For significant mortality to have occurred it has to be assumed that the iterative multiple-release-recapture model has underestimated this parameter to an extent which obscures both initial tag loss and the level of tagging mortality.

The analysis performed with the model, which suggests little if any tagging mortality, is consistent with the following observations made during the study which suggested that the tagging process was unlikely to have had a major impact on the abalone:

- a. The tagging technique was not observed to damage the soft tissues abalone and tagged animals rapidly cemented the tags into place with nacre.

- b. The direct effect of blocking a respiratory pore with a tag also appeared to be minor

as *H. rubra* are extremely flexible in their use of respiratory pores. This is illustrated by the fact that while the number of open and functioning respiratory pores was normally 6 it ranged from 1-7. The respiratory pores of the abalone are often interfered with naturally and in over 40% of the abalone handled the formation of respiratory pores had been disrupted by the attachment of a limpet which appeared to live commensally on the shell of the abalone. This disruption by limpets often caused the complete closure of one or more respiratory pores.

c. Only 318, or 3.5%, of the 9 015 abalone tagged during the study had their feet cut during handling. The recapture rate for these injured animals was 27.7% compared to 33.6% for uninjured animals. These figures suggest that while injury during tagging may have decreased the survival rate of some individuals it is unlikely to have had a significant effect on the results of the study.

d. Empty shells found during searches were examined for tags and collected if they were found to have tags. Only 38 of the empty shells examined were found to be tagged, clearly this is not enough to account for the rate of natural mortality documented by this study let alone being enough to suggest any additional tagging mortality.

It was expected that the boat tagging technique, involving extra handling and exposure abalone to the atmosphere, would affect the abalone to a greater extent. However, while some variability was evident, there was no consistent difference between the recapture rates of abalone tagged in the boat and those tagged *in situ* (Table 4.8). Proportionately more boat tagged than *in situ* tagged abalone were recaptured from the first and fourth recaptures, while *in situ* tagged abalone from the last release were recaptured proportionately more frequently than boat tagged abalone. These data do not support the hypothesis that the extra handling associated with boat tagging caused increased tagging mortality amongst boat tagged abalone.

4.4.2 Natural Mortality

The rate of decline due to tag loss and mortality, estimated by the revised version of the multiple-release-recapture model was 0.035 month^{-1} which corresponds to an annual instantaneous rate of 0.43. If the instantaneous rate of tag loss (0.15) is taken into account, an instantaneous annual mortality rate of approximately 0.28 or 75% survival between years is indicated. This mortality rate is slightly lower than those suggested by the data from the single release and recapture study, which showed that the instantaneous rate of decrease was 0.60, if recapture rates were corrected to account for changing

vulnerability of tagged abalone to recapture, or 0.61 if uncorrected data were used. Subtracting the instantaneous rate of tag loss from these rates gives mortality rates of 0.45 and 0.46 respectively, or 64 and 63% survivorship between years, respectively. Within the error structure of these estimates the difference of 12% is probably not significant. However, it is interesting to note that the initial versions of the iterative multiple-release-recapture model produced estimates of mortality that were considerably higher than the final estimate. From the discussion above (v. 4.3.2.d & 4.4.1.a) it is apparent that this was related to the constraints applied to other parameters in the ultimate version of the model and it is possible that a more precise description of sighting probability would have produced higher estimates of mortality. Consequently, the higher estimate of mortality should probably be preferred.

Table 4.8 Comparison of recapture rates of abalone tagged during each release period using boat or *in situ* tagging techniques. Only abalone expected to have obtained the legal minimum (v. 4.3.3.d) included in this comparison.

Date	Cut-off Length	Boat Tagging		<i>In situ</i> Tagging	
		Tagged (n)	Recapt.(%)	Tagged (n)	Recapt. (%)
Feb. 1985	86.5	705	14.8	286	9.8
Nov. 1985	102.9	-	-	819	19.3
Jun. 1986	116.8	1259	28.6	-	-
Oct. 1986	122.4	430	69.3	987	33.0
Mar. 1987	128.1	2196	40.6	855	41.5

The level of mortality observed during this study can be assumed to be the level of natural mortality amongst the emergent population as there is no evidence of any other influence on abalone abundances during the course of the study. The research site was legally closed to all fishing activity during this study and a considerable body of anecdotal evidence suggests that the local fishermen complied with, and supported this ban. The level of movement observed during this study also suggests that movement of abalone away from the research site was not significant. This assumption is supported by the fact that despite requests, divers diving on the reefs around George III Rock during this study returned no tags from abalone released in this study, although they returned tags from previous studies.

These estimates of natural mortality (0.28 & 0.45) for the emergent population are consistent with the results of Chapter 2 (v. 2.4.3) which documented high rates of

mortality for the youngest age classes, but lower rates for the older or larger size classes. There are two previous estimates of natural mortality for *H. rubra* contained in the literature, 0.20 and 0.36 (Beinssen & Powell 1979; Shepherd *et al.* 1982) which are reasonably compatible with those from this study. The estimates from this study are also reasonably consistent with the estimates (0.1-0.58) contained in the literature for other species (Doi *et al.* 1977; Sainsbury 1982a; Shepherd *et al.* 1982; Fournier & Breen 1983; Shepherd 1986a), although slightly towards the upper end of the range of estimates contained in the literature.

There is something of a trend running through studies of natural mortality in abalone populations; most earlier studies found relatively low levels of natural mortality while more recent studies have produced higher estimates. The estimate of 0.43 produced by Doi *et al.* (1977) for a Mexican haliotid species, was extremely high for that period and its veracity was questioned for that reason (S.A. Guzmán del Prío, pers. comm.). However, recently Shepherd (1986a) has documented a mortality rate of 0.58 for *H. laevigata* and G. Hamer (pers. comm.) has observed a similar level for *H. rubra* in New South Wales (Australia).

I postulate that this trend towards higher estimates of natural mortality is linked to the fact that in haliotids mortality is size or age related (v. 2.3.3). All previous mortality studies have concentrated on the exploited or emergent populations which, with time and the development of fisheries in most parts of the world, can be expected to have changed in their age composition. It follows that earlier studies were probably dominated by older age classes while more recent studies have examined younger populations. This explains the higher estimates being produced by current studies.

4.4.3 Population Analysis

The y-intercept of the relationship between the proportion of tagged abalone recaptured and time at liberty is the proportion of abalone that would have been recaptured if ongoing tag loss and mortality were both zero (v. 4.3.3.d). This proportion is determined only by the effectiveness of the recapture process, initial tagging mortality and initial tag loss. Accepting that the probability of recapture can be modelled with the parameters derived above (v. 4.3.2.d), this proportion can be calculated to be 55%. If it is also accepted that tagging induced mortality was minimal and initial tag loss was between 5 and 19% it can be estimated that between 58 and 68% of the abalone that were alive and tagged at the time of the final search were actually recovered. Given that a total

of 18 403 legal sized abalone were caught and searched for tags during the final recapture this proportion suggests that there were between 27 064 and 31 729 legal sized abalone in the population at the time of the final search commenced.

The validity of these estimates depend to some extent upon a series of assumptions. The first of these is that untagged abalone were as vulnerable to being caught as tagged abalone. If untagged abalone are less vulnerable than tagged abalone the population size will be underestimated; the converse will occur if untagged abalone are more vulnerable to capture than tagged abalone. There is no apparent reason to suspect that untagged abalone were more catchable than tagged abalone, however, the converse cannot be entirely discounted and may have caused some bias in these estimates. My observations suggest that the long term catchability of tagged abalone was similar to that of untagged abalone. Tags were observed to become completely overgrown with marine growth within 12 months and abalone at liberty for this length of time often had to be scraped around the respiratory pore to determine if they were tagged. In several cases tagged abalone were actually re-tagged underwater because no tag was initially detected; in these instances the double tagging was not discovered until the final recapture. This suggests that these estimates of population size should be relatively unaffected by this source of bias.

However this last observation raises the possibility that recaptured abalone may have gone undetected at the final recapture. If the probability of detecting tags during the final recapture declined significantly with their time at liberty, estimates of natural mortality and population size derived by this study could be too high. Again, this may be a factor affecting these results, but the magnitude of any under reporting is likely to have been small. All the abalone caught during the recapture were examined individually by experienced research personnel who had instructions to scrape clean the respiratory pores of every shell.

Another potential source of bias in these estimates involves the assumption of uniform mixing. In order to provide unbiased estimates of population density tagged animals need to be mixed uniformly through the population. Clearly the movement patterns documented in this study preclude random mixing of tagged animals through the population. Boat tagging was conducted throughout the research area in an attempt to distribute tags through the population, and an attempt was made to distribute the tags in relationship to the distribution of the population. However the detailed census of the population that would be required to accurately plan or assess this strategy was beyond the scope of this study. Data presented in Table 4.8 indicate some variability in the recapture rates of

different releases undoubtedly indicating localized patterns of release and recapture and indicative of non-random mixing. This suggests that this study would be most prone to bias from this source, but from these data, it is not possible to predict the level of bias or whether the bias would have been higher or lower. Results presented in Section 5.3.2 indicate that the tagging study was reasonably successful in distributing tags through the area in rough proportion to the population distribution. Additionally, it is evident that the most of the population was concentrated in the shallow region of the research site where the rates of movement were greatest. Consequently a relatively high degree of random mixing probably did occur through the majority of the population and this portion of the population can be expected to have dominated these results. Thus, I believe no serious bias is likely to have arisen from this source.

For these reasons it seems likely that the actual population of legal size abalone on George III Rock at the time of the study was approximately 27 000 – 32 000.

4.4.4 Growth and Reproduction

When the t_0 of 2.4 years, derived from the ageing data, is used with the von Bertalanffy curve, derived from the tagging data, there is close agreement between the two different growth equations (Fig. 4.7) for the size range of animals tagged (89–166 mm). For the entire size range of the population the Gompertz equation is clearly the better description of growth. However over the size range that I tagged (the emergent population), a visual inspection suggests that the von Bertalanffy equation apparently passes closer to the length at age data points than the Gompertz equation. These results support those from Chapter 2 (v. 2.4.2) which indicate that the use of a single von Bertalanffy curve derived from a tagging study, to describe both adult and juvenile growth could cause a significant over-estimation of juvenile growth. For example if a t_0 of zero was assumed for this growth curve, in the same way Harrison and Grant (1971) did, the age of an abalone at maturity would be under-estimated by 2.4 years.

Recently, Francis (1988) has suggested that growth parameters derived from tagging and age-length data are simply incomparable and cannot be reconciled within a single von Bertalanffy curve. This is due to the fundamentally different nature of these two types of data and the variability of growth between individuals of any natural population. Francis predicts that the difference between curves estimated using each of the two types of data will increase with age, and that tagging data will produce a higher estimate of L_∞ than age-length data. The L_∞ estimated for the George III Rock population using age-length

data was, in fact, marginally lower than that estimated by the tagging data, as predicted by Francis.

The difference in juvenile growth estimated by the two curves in this study is, however, not explained by Francis' thesis. This difference is because juvenile and adult growth cannot be described by a single von Bertalanffy curve. The von Bertalanffy equation implies a smooth convex growth curve such that the time taken for the mean length of a size class to grow halfway from any starting length to L_{∞} , is $(\log_e 2)/k$ (Francis 1988). At both Blubber Head and George III Rock the growth curve during the juvenile phases was more accurately described with a straight line or downward inflexion. Clearly this shape cannot be reconciled within the inherent shape of a von Bertalanffy curve.

The results presented here indicate some intra-specific variability in growth. The George III Rock site and Blubber Head site are only separated by *c.* 25 km of sea yet the estimated L_{∞} or average maximum size for the population varied by approximately 15 mm (George III Rock=154.7 (s.e.=0.72) and Blubber Head=139.7 mm (s.e.=7.24)). The instantaneous rate of increase, K , also varied greatly between the two sites being estimated as 0.288 (s.e.=0.037) at Blubber Head and 0.471 (s.e.=0.021) at George III rock indicating a higher growth rate for abalone at the latter site.

The size of first maturity also varied between the two sites being approximately 90 mm at Blubber Head and about 110 mm at George III Rock. The implication of the different growth rates and sizes at maturity is that despite the different growth rates the abalone at the two locations mature at a similar age and stage of the growth curve. In both locations growth of juveniles is apparently relatively linear until about five years of age when some individuals in the population begin to mature and after which the curve conforms to a standard von Bertalanffy form.

4.4.5 Population Structure

While the anaesthetic sampling technique was of limited efficiency at George III Rock it still indicated that the youngest age classes of abalone were relatively abundant when compared to the mature population (Fig. 4.5). This was also implied by the age structure of the emergent population and the mortality rates documented in this study. The density of the emergent population was measured at 0.50 ab.m^{-2} during the $15 \times 15 \text{ m}^2$ search (Fig. 4.6a) and approximately 20% of these animals were 9 y-old abalone (Fig. 4.6b).

Using an approximate annual survival rate of 70% (rather than the lower rates suggested by Chapter 2 (v. 2.3.3)) a minimum density of this year class at each previous age can be back calculated. Assuming a population with recruitment that is stable at the level which produced the 9 y-old year class, it is possible to sum the year class densities and estimate a total population density for the cryptic juvenile abalone (<7 y-old). Following this procedure the density of cryptic abalone can be estimated at 9.3 ab.m⁻² which suggests that numerically they could comprise approximately 95% of the population.

It should be remembered that a constant survival rate of 70% has been used in this calculation, although the results of the Blubber Head study suggest much higher mortality rates may apply to these younger animals. If lower survival rates were used, the juveniles would be found to constitute a much larger numerical proportion of the population than this estimate indicates. These estimates indicate the degree to which the cryptic population was under-sampled in the anaesthetic samples and the extent to which the emergent larger size classes dominate the sampled population because they are visibly obvious at George III Rock.

The structure of the emergent population at George III Rock supports the finding of Chapter 2 (v. 2.4.4) that for *H. rubra* emergence is linked with sexual maturity. The data show that the emergent population was predominantly composed of mature abalone (Fig. 4.8) from a number of year classes (Fig. 4.6b). Their appearance as a single mode in the length–frequency histograms is due to the coalescing of age classes as they approach the asymptotic size for the population (Fig. 4.7). This is another feature found to be in common with the population at Blubber Head.

The three year classes that dominated the emergent population on George III Rock (7–9 y-old, Fig. 4.6a) do not show the decline in abundance with increasing age that may have been expected to result from a natural mortality of 0.29–0.47 (52–75% survival). This could be attributed to any combination of three possible factors: errors in the ageing of animals; declining levels of recruitment during the period in which these year classes were spawned; or the recruitment of each age class to the emergent population occurring over an extended time span. As there would appear to be little biological reason to propose knife-edge entry to the emergent population, the last factor is almost certainly involved to some degree. An extended window of time over which recruitment occurs is suggested by the fact that some 4–6 y-old abalone were found in the emergent population. This population structure and the data regarding sexual maturity are consistent with the hypothesis that individuals mature between 4 and 10 y of age and emerge as they mature.

Because the emergent abalone are highly visible compared to the cryptic population the fishery concentrates exclusively on the emergent population and emergence is tantamount to recruitment into this fishery. Of course, because there is a size limit of 132 mm in the Tasmanian abalone fishery, where emergence occurs below this size, recruitment to the fishery will be delayed until the abalone attain the legal minimum size. However at sites such as George III Rock where most of the emergence occurs at or above 132 mm, emergence and recruitment to the fishery are synonymous.

4.4.6 Movement and Feeding

The movements observed during this study were considerably greater than anticipated and, in retrospect, much of the permanent transect structure was of limited use because of this.

Most authors have recorded little or no movement among the various species of abalone (Momma & Sato 1969; Poore 1972a; Clavier & Richards 1984). Previous studies of *H. rubra* have also found limited movement patterns: Shepherd (1973) suggested that while *H. rubra* was the most mobile of the southern Australian haliotids its movements were limited to a scale measured in metres; Beinssen and Powell (1979) found that in the Victorian population of *H. rubra* they studied <10% of the individuals moved >50 m in a 2 year period; in Tasmanian populations at Blubber Head and Maria Island, it has been found that abalone generally moved <20 m over a year (R.White & P.Whyte pers. comm.). It was this body of information which was used in the design of this experiment.

However some studies for other haliotid species have been published documenting more extensive movement patterns. Newman (1966) documented an annual mean movement of approximately 1000 m in the South African species *H. midae*, while Shepherd (1986a) found that the modal distance moved after 6 months at one particular site, by the South Australian species *H. laevisgata*, was 25–30 m, and the maximum 250 m. Ault and Demartini (1987) also observed a high degree of mobility by *H. rufescens*. The movement patterns described in these studies are compatible with those I observed at for *H. rubra* at George III Rock and clearly demonstrate that haliotids are capable of relatively extensive movement.

The results of this study show that movement in *H. rubra* at this site can be thought of as a relatively random diffusion process with the rate of diffusion being dependent upon habitat, direction and size. These factors have all been discussed previously in the literature as influencing movement in other species. Shepherd (1986a) proposed that

movement was strongly related to the availability of crevices, which are used by the abalone for protection against predators and as natural collectors of drift algae on which they may feed. Shepherd (1986a) also presented data showing movement that was orientated towards the direction of the prevailing swell, as did Clavier and Richard (1984). A number of studies have found that the rate of movement is size related; Newman (1966) and Shepherd (1986b) found that movement is less amongst smaller individuals while Clavier and Richard (1984) observed the opposite.

At George III Rock smaller individuals within the emergent population were clearly less mobile than larger individuals (Fig. 4.14). Shepherd (1986a) suggested that because of their size, there would be more crevice habitat available to smaller abalone than to larger individuals and, thus, they would be less likely to disperse long distances. However this phenomenon could be mediated by other factors. The decline of mortality rates with size or age (v. 2.3.3) suggests that a large size offers abalone a refuge from predation. One of the main forms of defence for abalone is a firm grip on the substratum and for this reason movement is likely to be inherently risky for abalone, particularly for small abalone. It thus seems logical to propose that smaller abalone may have developed risk minimizing behaviour which makes them less likely than larger individuals to move in response to the same feeding or breeding stimuli. For this reason it is possible that size related movement is a direct behavioural response which interacts with environmental conditions such as crevice availability, rather than a purely physical interaction with the environment as suggested by Shepherd.

I did not collect quantitative data on the comparative availability of crevice spaces between the different habitats so I can not definitely exclude this factor as being a causal agent for the movement patterns in the different habitats. However my qualitative observations suggest that in the deeper water habitat, where the least movement occurred, there were less crevices available as the substratum tended to be sparsely spread boulders sitting directly on sand. In contrast, in the *Durvillaea* habitat where I observed the highest level of movement, crevices appeared to be more abundant because several layers of boulders were lying on top of a solid stratum of bedrock.

Hunger has also been suggested as a causal agent of movement by Poore (1972a), Hines and Pearse (1982), and Ault and Demartini (1987). The results of this study suggest that the observed habitat-related movement may be mediated by food availability. In both segments of the tagging study movement was found to be higher in the *Durvillaea* habitat (Fig. 4.14, Table 4.4). The *Durvillaea* habitat was characterized by

the low abundance of the fleshy rhodophytes, a food item which was extremely important in the diet of the abalone in all habitats. In the *Durvillaea* habitat the abalone exhibited strong selectivity for the fleshy rhodophytes (Fig. 4.9b), suggesting that the greater level of mobility in this habitat was associated with a greater need to search for the preferred food. The suggestion that the abalone found it more difficult to find the desired food items in the shallower habitat is supported by the gut index information which shows that abalone in the *Durvillaea* habitat had proportionately less in their stomachs than in the deeper water habitats where the fleshy reds were more common and movement was considerably less (Fig. 4.9a).

The multiple release-recapture data collected during this study found that movement tended to be directional with regard to depth. Movements towards shallower positions were more likely than towards deeper positions. Shepherd (1986a) and Clavier and Richards (1984) observed directional movements towards the direction of the prevailing swell. I found that abalone moved towards shallower positions regardless of whether or not this coincided with the movement into approaching swells. This does not necessarily prove that the abalone at this site are not exhibiting movement patterns orientated towards the swell, but it does show that, at this site, the tendency to move towards shallower water was more important. The two previous studies indicating the importance of swell direction present little information regarding depth changes and because of this the possibility of interactions between depth and swell direction in their studies can not be gauged.

Abalone have been observed to move towards higher positions during spawning (Quayle 1971; Breen & Adkins 1980) and conceivably such behaviour could benefit the abalone in a number of ways. The first is that by climbing above other members of a spawning population a female could ensure her eggs fall a greater distance through the cloud of male gametes being broadcast by the males, maximizing the chances of her eggs being fertilized. As suggested in Section 3.4, movement towards shallower water may also maximize the probability of ensuring that eggs are cast onto hard substrate rather than onto sand.

Shepherd (1986b) observed aggregative behaviour in *H. laevisgata* which was associated with the breeding cycle of that species, and he suggested that such behaviour could have the adaptive advantage of maximizing the success of broadcast spawning. Movement towards shallower water on a coastal reef could be an aggregative mechanism which leads to the aggregation of *H. rubra* on the higher points of reefs, maximizing the

effectiveness of any broadcast spawning event. If this hypothesis is correct, whether or not the point at which the abalone aggregate is shallow or deep may be immaterial; what is probably important is that the population shares the same responses to the same cues, allowing them to move towards the same point. It is possible that the movement of *H. laevigata* in relation to the direction of prevailing swells (Shepherd 1986a) provides the mechanism by which that species forms aggregations. *H. laevigata* generally select deeper water sites than *H. rubra*, being commonly found in aggregations along the sandy edges of reefs (Shepherd 1973). Movement into the prevailing swell would generally cause an abalone to move seaward and down towards the sandy edges of the reef, so it could be a cue by which individuals of that species orientate and are able to move towards a common area of a reef in order to form aggregations.

I hypothesise that the two forms of movement documented by this study viz., random foraging driven dispersion and the aggregative directional movements, play a fundamental role in regulating abalone populations. The foraging movement may provide the mechanism by which abalone populations disperse as food resources become limiting, while the directional movement may ensure that sufficient aggregations exist to ensure successful reproduction.

4.5 CONCLUSIONS

This study of the general biology of the abalone population at George III Rock confirmed or supported many of the results of the Blubber Head study (Chapter 2). The juvenile population is extremely abundant compared to the adult population, although extremely difficult to sample because of their cryptic nature. Emergence from the cryptic habitat apparently coincides with the onset of maturity. At George III Rock and Blubber Head this is between the ages 4⁺ and 9⁺. At George III Rock abalone emerge at about the size of the legal minimum size so that emergence is tantamount to recruitment into the fishery.

Comparison of growth at George III Rock with that at Blubber Head shows that it is considerably faster, and the asymptotic length of the population much larger, at the former site. Interestingly, despite the different rates the general form of the growth curve is similar between sites: growth is almost linear until the onset of maturity at about 5 y-old and cannot be described with von Bertalanffy parameters; the growth of mature abalone can be described by von Bertalanffy parameters and approaches the asymptotic length of the population at about 12 y-old.

Mature emergent abalone have relatively high survival rates (62-75% annum⁻¹) and the emergent population is composed of a large number of year classes. However because they are mature animals with slower growth rates the size distributions of the different year classes coalesce so that the length-frequency histogram for the emergent population is uni-modal.

Two types of movement were observed within the emergent population at George III Rock. The first is relatively random foraging behaviour, the magnitude of which is related to food availability. This movement of itself would result in the simple diffusion and dispersion of abalone through the habitat. However the second type of movement was a directional movement towards shallower water. This movement apparently leads to the aggregation of abalone on shallow areas of reef which I hypothesise may be important for the breeding success of this species. Together these movement could play an important part in the natural regulation of abalone populations, leading to either dispersion or aggregation in response to changing population size and the relative abundance of food.

CHAPTER 5

A PRACTICAL SHORT TERM STUDY OF THE FISHERY FOR *HALIOTIS RUBRA*.

5.1 INTRODUCTION

A fishery by definition involves an interaction between humans and some exploited species. Thus a study of the fishery biology of any species must at some point touch upon the interaction of humans and the particular species. Generally this point of interaction involves one of the most fundamental assumptions of fisheries science: that catch per unit effort (CPUE) reflects stock abundance. To date the status of the abalone fisheries of Australia have been assessed upon this assumption (Ward 1986) although the validity of this assumption has never been scientifically assessed. It is generally accepted that this relationship can be greatly affected by both the human part of the fishery, such as the manner by which fishermen allocate their effort (Russell 1931) and factors in the biology of the fished species, such as the spatial distribution of species (Hilborn & Walters 1987). The primary aim of Chapters 5-7 is to examine the interaction between the biological nature of *Haliotis rubra* and the human aspect of the Tasmanian abalone fishery in order to assess the usefulness of CPUE data in this fishery.

In this chapter I describe a Leslie-DeLury type fish-down experiment which I conducted in order to study in more detail, both quantitatively and qualitatively, the interaction between the biology of abalone and abalone divers on the scale of a single reef and a few days. In Chapter 6 I draw the different aspects of abalone biology and diver behaviour together within a model of a single exploited population in order to examine the results of this and preceding chapters in a more theoretical way, and to postulate about the relationship between CPUE and stock abundance on a wider temporal scale. In Chapter 7 I present a description of the Tasmanian fishery for *H. rubra* and examine the factors that may have influenced the observed trends in CPUE.

5.2 METHODS

5.2.1 Field Work

5.2.1.a Fish-down Experiment

The research site used in this experiment George III Rock, has been described elsewhere (Section 4.2.1). In July 1987 commercial divers wishing to take part in this fish-down experiment were invited to put their names into a ballot from which four were randomly selected. Two of the selected divers (divers 1 & 4) had never dived within the research area, one (diver 3) had dived in the area on one occasion prior to it being closed to commercial activities; the fourth (diver 2) had fished some sections of the area on an occasional basis prior to its closure. A commitment was given by each diver to continue

fishing in the area for at least six diving days. The divers were asked to follow their normal diving practice and determine their own diving patterns within the restrictions of the experiment. The main restriction was that they agree to work a standard diving day of 6 h duration. The experiment was conducted between 7 July and 3 August, 1987 and a total of 7 days were dived. All the divers completed the first six days of diving, one of the divers (diver 1) was prevented from diving on the seventh and final day due to family commitments. The actual days on which diving took place were selected by mutual consent on the basis of the suitability of weather.

The normal commercial diving practice in the Tasmanian abalone industry is for each diver to dive from their own 4-7 m diving vessel. The diver's air is supplied through an air hose connected to a compressor powered by a small petrol engine aboard the boat. This compressed air equipment is known as a 'hookah'. The vessel remains under power while the diver is underwater and follows his path as he swims. A deckhand is employed to keep the vessel as close as possible to the submerged divers and to keep the air hose from fouling in the kelp. Normally the deckhand will keep the vessel within 20 m of the diver at all times. The diver swims freely underwater carrying a bag in which he places the abalone; the bag will hold up to about 80 abalone. Generally, a diver surfaces only to bring a bag full of abalone to the surface and collect an empty bag.

An observer familiar with the research site was aboard each diver's vessel throughout each day of fishing. The observer recorded the diver's activity and monitored the diver's position by taking bearings from two dan poles moored at known points on the permanent transect which had been laid through the area (v. 4.2.4.a). The observers noted the following activities and the time at which they occurred:

- a. diver submerging,
- b. diver surfacing,
- c. bags of abalone being brought to the surface, and
- d. empty bags being taken to the bottom.

Bearings were taken on both dan poles each of the above and at regular (5-10 min.) intervals when the diver was submerged. Bearings were taken more regularly if the diver changed positions rapidly.

The observers also recorded the number of abalone in each bag brought to the surface, and searched for tagged abalone, recording in which bag each tagged abalone was found. Length-frequency data were collected by each observer where possible for approximately 100 abalone each day from both the *Durvillaea* and *Macrocystis* habitats.

5.2.1.b *Independent Assessment of Density*

Prior to the fish-down experiment a 15 x 15 m area had been searched by research divers who collected and measured the length of all the emergent abalone (v. 4.2.2.a). After the fish-down experiment two more 15 x 15 m areas were selected close to the original area, and the procedure repeated.

5.2.2 Analysis

Catch rates ($\text{ab} \cdot \text{min}^{-1}$) have been estimated, as hourly summaries and for each bag of abalone. Hourly summaries have been used to examine catch rate over the entire research area and have been estimated using the total time spent submerged during any hour of the experiment (min) and the total catch (ab) taken during that hour. Catch rates per bag have been used to examine trends within individual areas of the research site and have been calculated using the number of abalone in a bag and the time spent submerged to collect those abalone.

In order to examine catch rate trends within individual areas of the research site the research area has been divided into 29 blocks on the following basis and priority:

- a. all blocks are approximately equal in area (125 x 125 m).
- b. each block is as homogeneous as possible with regard to habitat.
- c. each block is as close as possible to rectangular.

These blocks are shown in Fig. 5.1 The bearings, times and other notes were used to trace the movement of each diver throughout the fish-down experiment. Typically, the path of a diver collecting a single bag of abalone was marked with 5-10 bearing points and times, including the start and end points. Assuming that divers move directly between each triangulated point at a uniform speed, the time elapsed between adjacent bearing points was used to calculate a time/distance relationship for each segment of each trace. Using this relationship, the time spent in each block during each segment of a trace was calculated, together with the total time spent in the block during the collection of that particular bag of abalone. Making the assumption that catch rates are constant during the collection of any particular bag of abalone the estimated total time in each block was then used to estimate the catch from each block for each bagful. All figures have been worked in number of abalone and minutes and these units apply throughout this chapter unless stated.

The techniques of Leslie and Davis (1939) rather than those of DeLury (1947) have

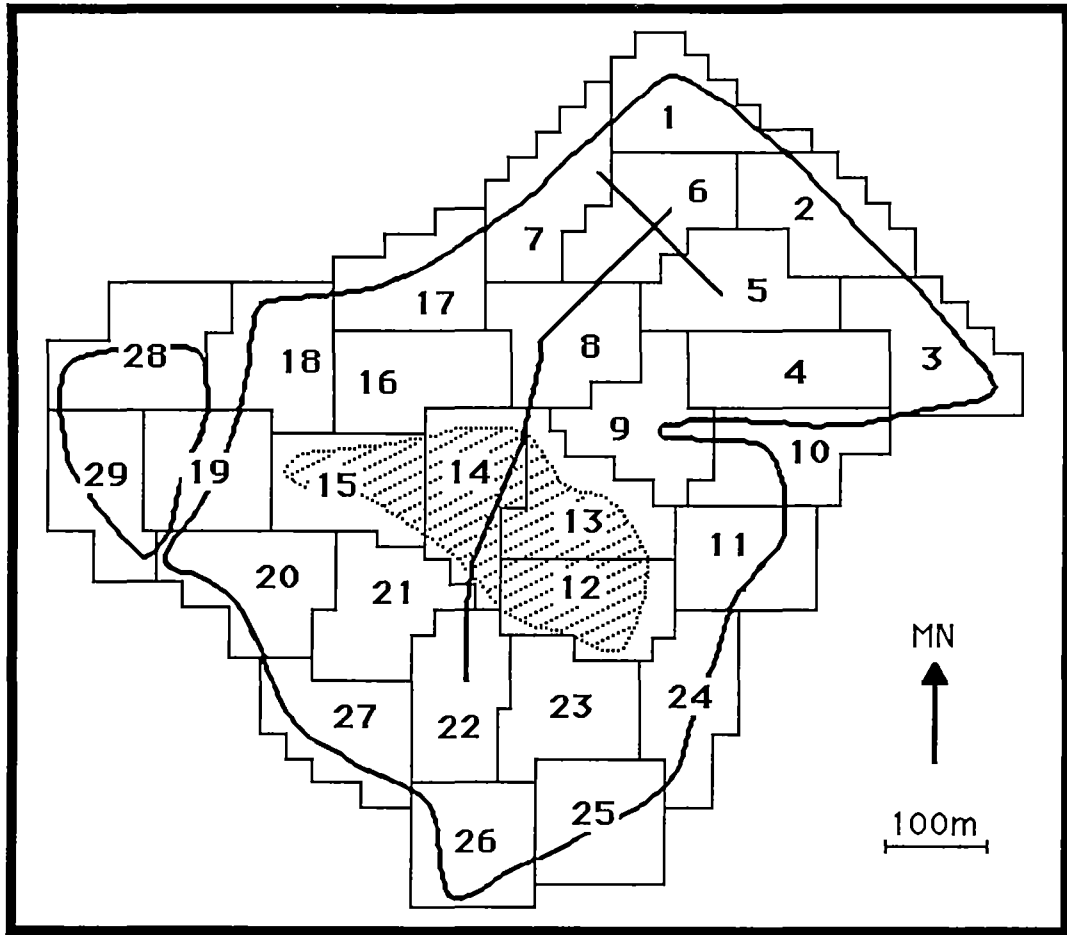


Figure 5.1
A map of George III Rock showing the blocks used to break down catch and effort data collected during the fishdown experiment.

been used with these data to produce population estimates as that technique is apparently less biased than the former technique (C.J.Walters, pers. comm.). The modifications of Leslie's technique suggested by Braaten (1969) have also been used. This involves using the estimated cumulative catch up until the middle of each period of effort rather than to the beginning.

5.3 RESULTS AND DISCUSSION

5.3.1 Fishing Patterns

The fish-down experiment was conducted over seven diving days with a total diving time of 48 h. During this time a total of 8 208 min were spent underwater by the four divers, and 18 403 abalone were captured (Fig 5.2a); an average catch rate of 2.24 ab.min^{-1} (Fig. 5.2b). Catch rates were initially $3.7 - 4.7 \text{ ab.min}^{-1}$ but declined to $0.7-1.5 \text{ ab.min}^{-1}$ by the end of the experiment (Fig. 5.2b). Throughout the experiment, the mean weight of the abalone in the catch was 500 g, therefore, multiplying the catch rates used in this chapter by 30 gave the more conventional catch rate unit kg.h^{-1} . A strong relationship was observed between the effort expended and the catch taken, both over the research site as a whole (Fig. 5.2a) and within the 29 individual blocks (Fig. 5.3).

The effort was not distributed over the research site randomly; 64% of effort was concentrated in blocks 12–15 (Fig. 5.4a) which were the four shallowest ($<10 \text{ m}$) blocks (Fig. 5.4b). These blocks contained approximately 14% of the reef area within the research site (Fig. 5.1). Figure 5.5 shows the spatial diving pattern of the divers over the 7 days of the experiment, with each point indicating that a diver entered a block at a particular time, as distinct from the amount of effort the diver expended in that block at that time. Therefore, Fig. 5.5 does not strictly show the allocation of effort over time and space; however the frequency with which divers entered any block approximates the levels of effort expended. The divers clearly targeted the central shallow blocks from the start of the experiment and almost no effort was expended outside of this area for the first 200 min of the experiment.

Where sufficient effort was expended, the catch taken and effort expended in each block during the initial and final 30 min of effort were used to estimate the initial and final catch rates (Figs. 5.6a & b). These estimates showed that the shallow blocks had the highest initial catch rates (Fig. 5.6a), an obvious reason for the divers targeting these blocks initially. However no commercial fisherman had dived in the research area since

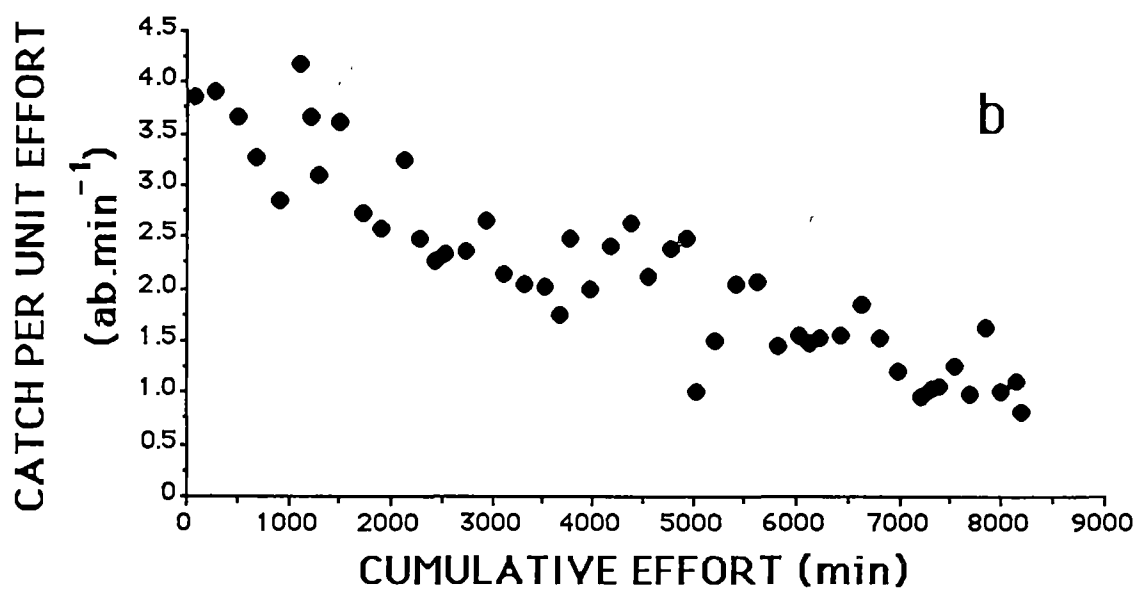
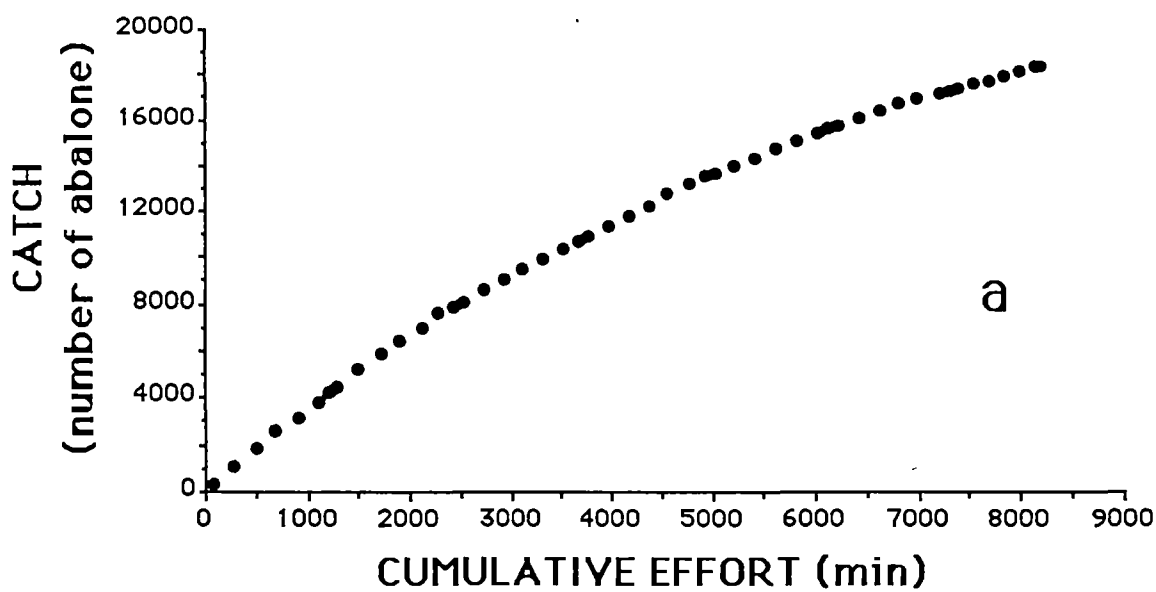


Figure 5.2
Cumulative catch (ab) made during the fishdown experiment at George III Rock (a) and (b) catch per unit effort (ab.min⁻¹) plotted against the cumulative effort (min).

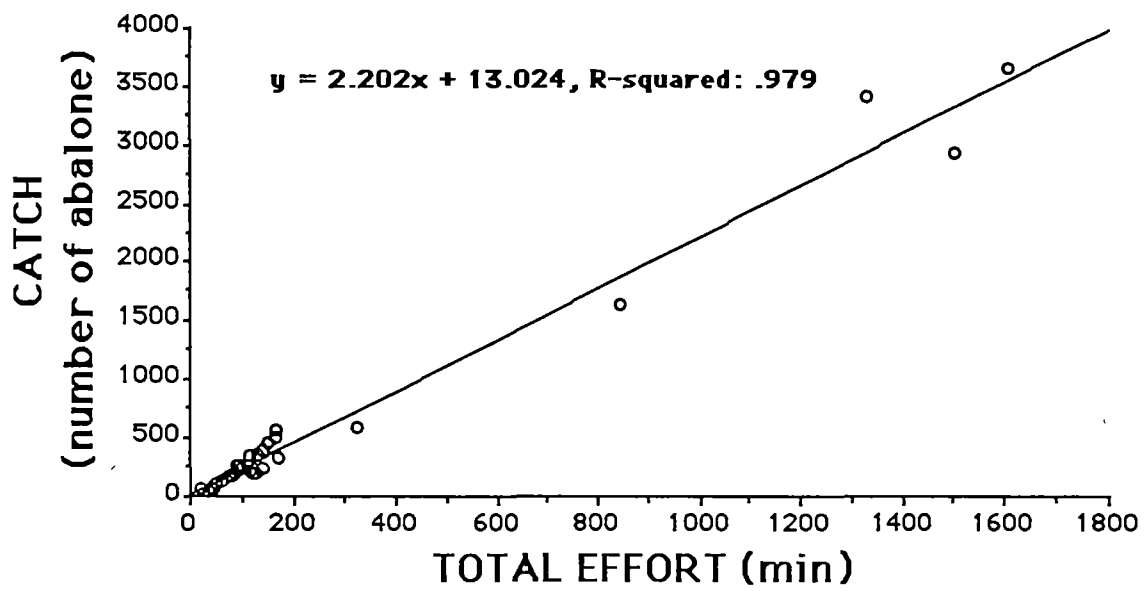


Figure 5.3
The relationship between total effort (min) expended in a block and the total catch (ab) taken from each block.

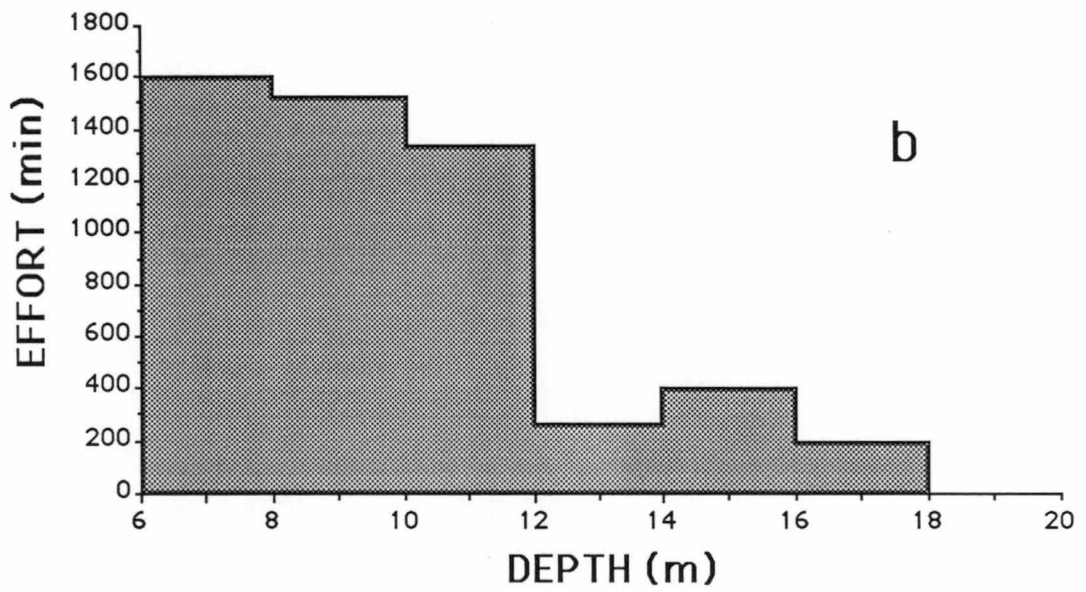
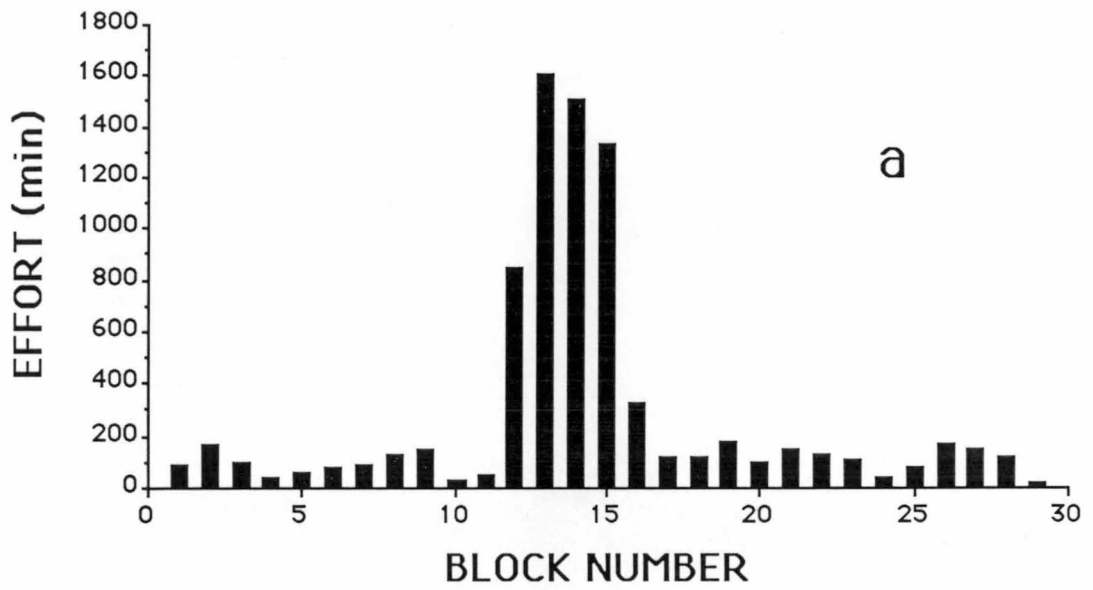


Figure 5.4
The distribution of effort (min) with regard to block (a) and depth (b).

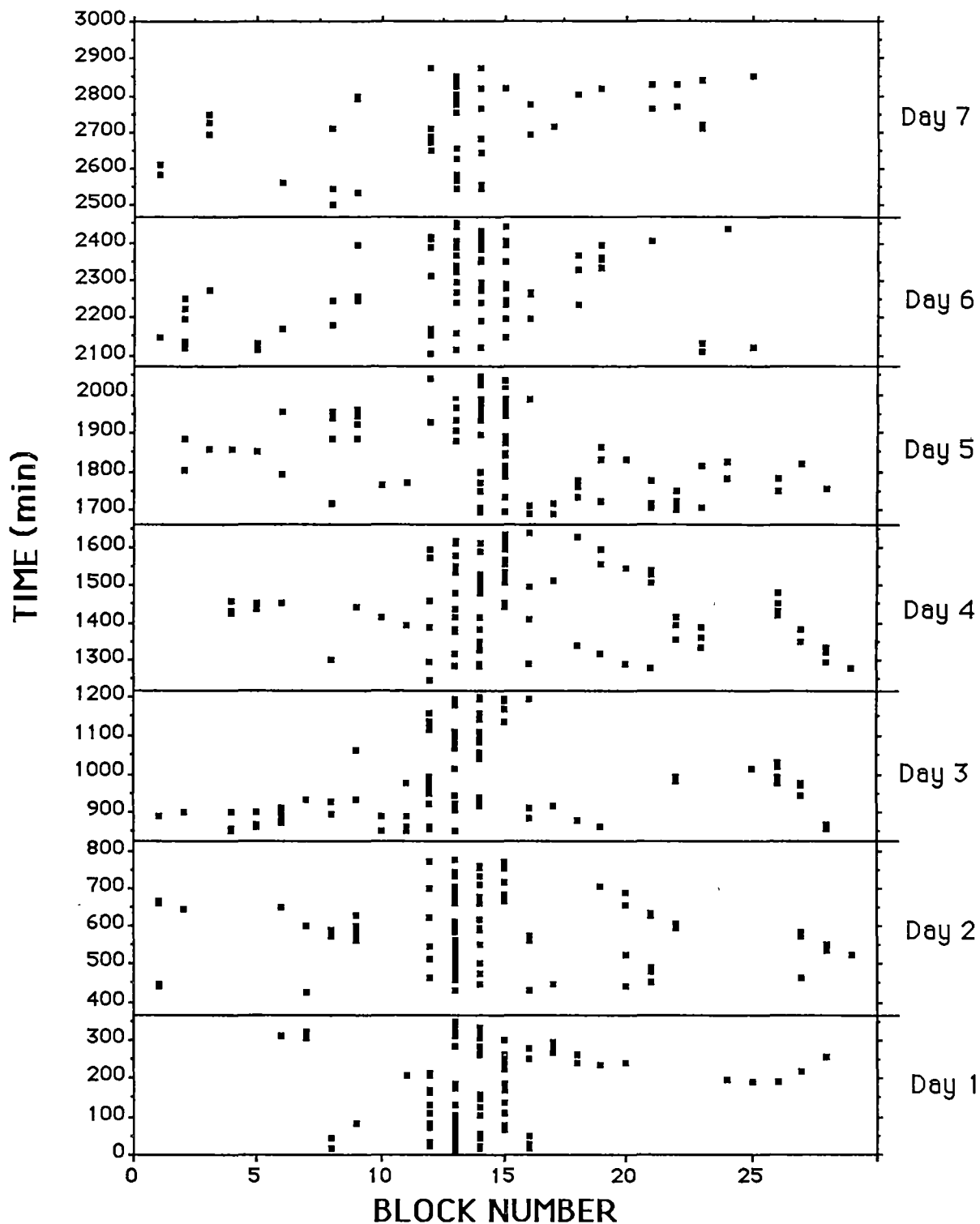


Figure 5.5

The spatial and temporal distribution of fishing effort during the fishdown experiment. Each point in this figure indicates a particular time during the experiment (day 1-7 or diving minutes 1-3000) when a diver entered a particular block (1-29). N.B. the points indicate only that a diver entered a particular block and not indicate the level of effort expended.

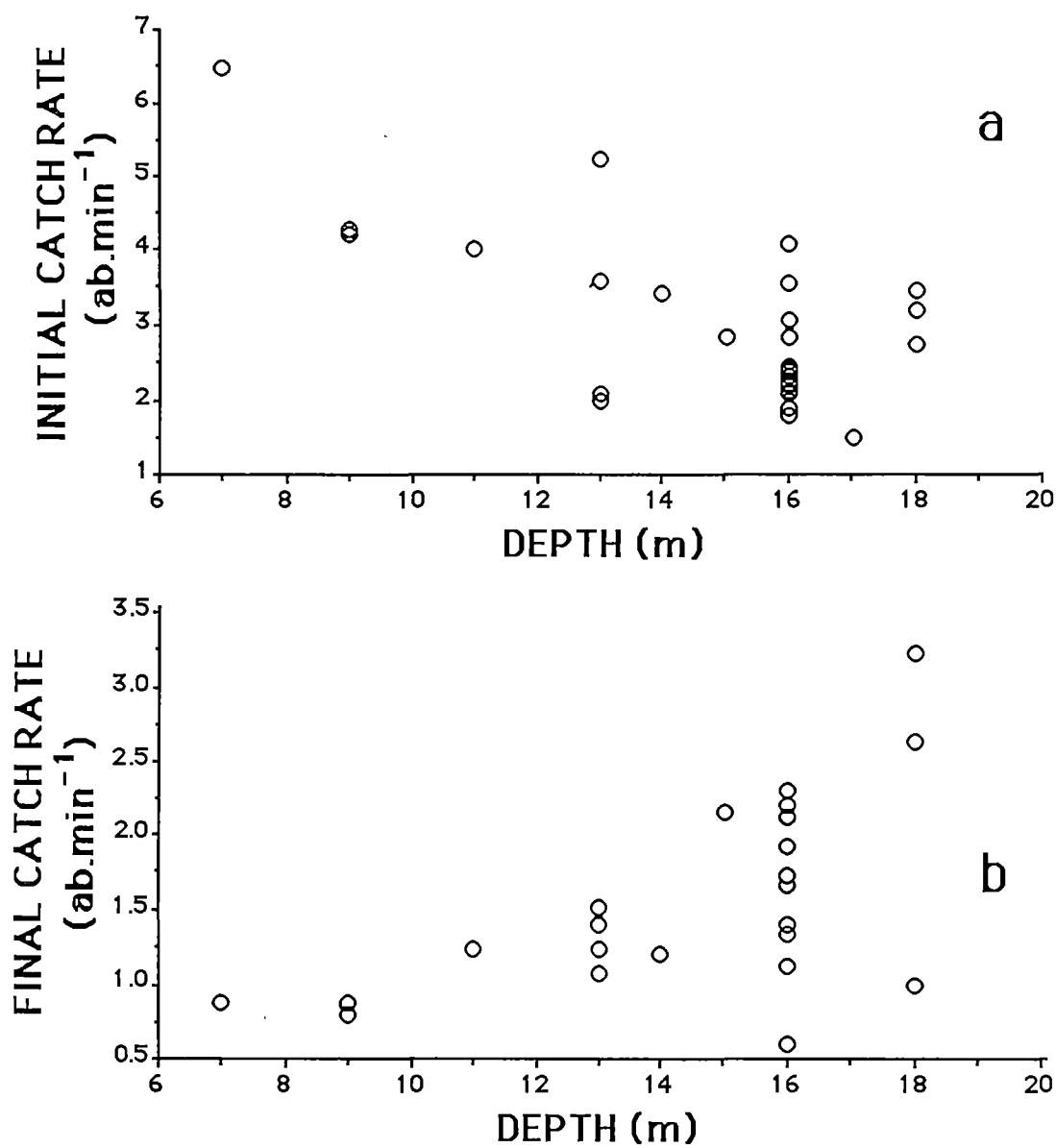


Figure 5.6

The relationship between the initial catch rate of a block (ab.min⁻¹ for the first 30 min of effort) and the average depth (m) of the block (a), and between final catch rate (abalone.min⁻¹ for the last 30 min of effort) and (b) average depth (m).

June 1984, and only one of the four divers (diver 2) had spent a significant amount of time diving in the area before its closure, raising the question of how the divers were able to identify and target the area with the highest catch rate from the first dive of the experiment (Fig. 5.5). Discussions between the observers and individual divers showed that prior to the experiment beginning each diver had independently identified the shallow *Durvillaea* habitat of the research site as the area that should provide the best catch rates at the start of the experiment, and planned to commence their fishing in that area.

Towards the end of day 1 the divers entered a few of the less central and deeper water blocks. On day 2 the divers initially concentrated on the shallow blocks but began using the less central, deeper blocks towards the middle of day 2. This increased activity outside the central, shallow blocks is reflected in the proportion of the catch and effort taken in depths <10 m, which declined slightly (Fig. 5.7a) during the second day. While the activity in deeper water increased during the second day it should be noted that a large proportion of this effort (40%) was expended by diver 2 (Fig. 5.8).

After day 1 the catch rates in the deeper blocks (>10 m) were always higher than in the shallow blocks (Fig. 5.7b). Despite the higher catch rates to be expected in deeper blocks, the divers continued to concentrate their effort in the shallower areas so that the final catch rates in the shallow blocks were lower than those in the deeper blocks (Fig. 5.6b).

Two reasons probably explain this bias. Diving is known to be dangerous to the health in the long-term and the danger is directly related to the duration and depth of diving. For this reason divers generally favour diving in shallow water, but in the short-term divers are restricted in their diving practice by the immediate need to avoid decompression sickness. The commercial divers of Tasmania rarely stop their abalone fishing to decompress in shallow water at the end of a day's diving; instead they plan their dives so that they finish each day in relatively shallow water. This is evident from Fig. 5.5; throughout the experiment divers concentrated their effort in the central shallowest blocks towards the end of each day.

Secondly, discussions with divers, together with searches made by research divers during the tagging program, showed that *H. rubra* in the deeper areas are generally concentrated on the sandy edges of reefs. However, their occurrence in this habitat is much more unpredictable and patchy than in the shallow water habitat. In the deeper blocks of George III Rock sand edges were relatively common in the peripheral blocks. However concentrations of abalone in the deeper blocks only occurred in blocks 1, 2, 3,

Figure 5.7a

The proportion of the catch (solid points) caught and effort (empty points) expended in depths <10 m during each day of the fishdown experiment.

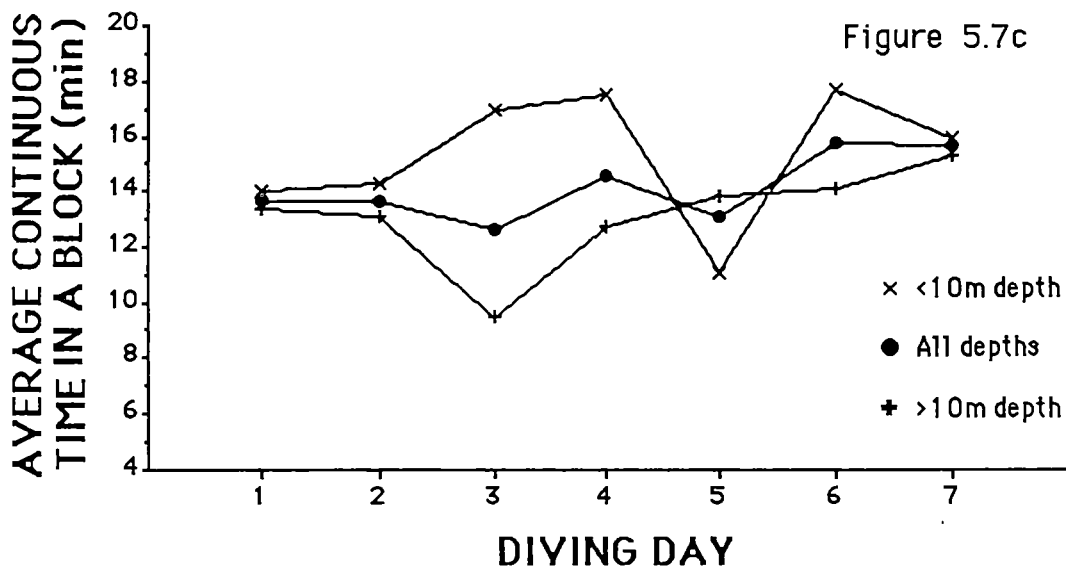
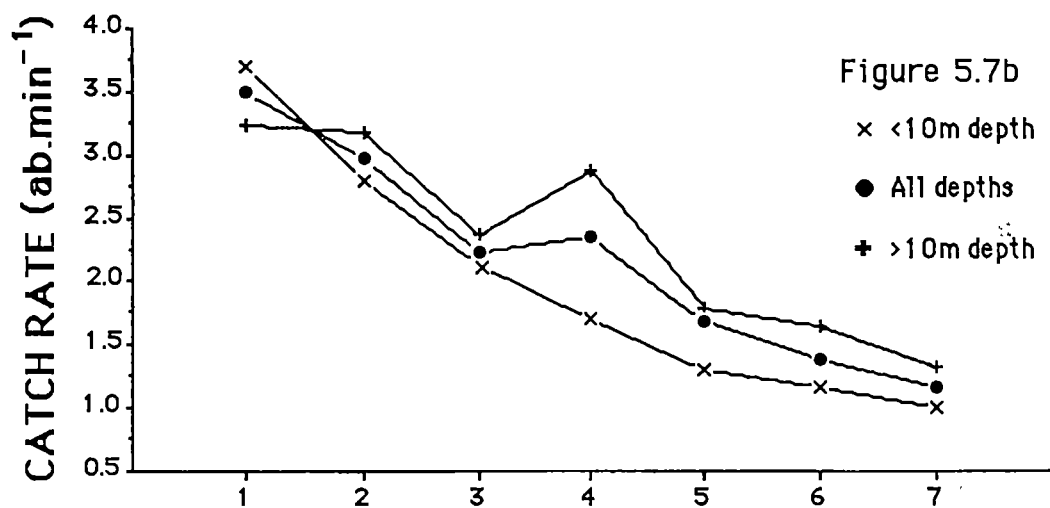
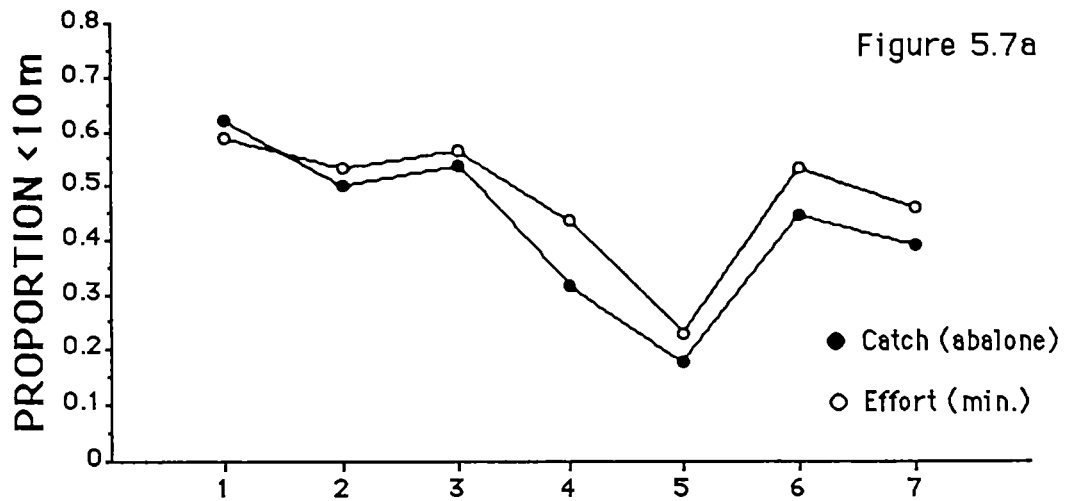
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Figure 5.7b

Average catch rate (ab.min⁻¹) during each days diving in blocks; with an average depth <10 m (x), with an average depth >10 m (crosses), all blocks pooled (solid points).

Figure 5.7c

Average continuous diving time (min) in each block; with an average depth <10 m (x), with an average depth >10 m (crosses), all blocks pooled (solid points) during each day of the fishdown experiment.



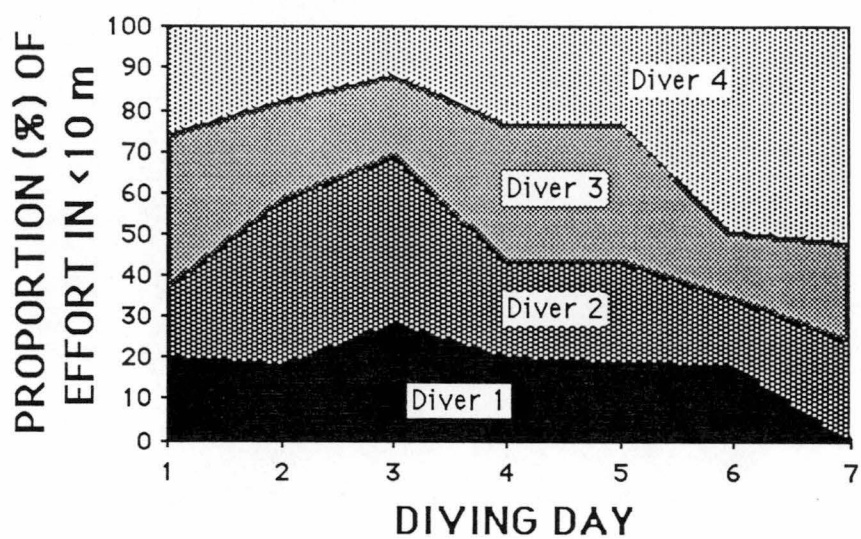


Figure 5.8
The proportion (%) of the effort expended during each diving day in depths >10 m, by individual divers.

8, 9, 19, 26, 27 and 28 (Fig. 5.1). This distribution pattern means that a diver without local knowledge must search fairly randomly for deep water concentrations and therefore increase the effective cost of diving in deeper water. Diver 2, who directed the greatest individual effort towards the deeper blocks during days 2 and 3 (Fig. 5.8) was the diver with prior experience of the area and was prepared to leave the shallow water and fish in deeper water at an earlier stage of the experiment than the other divers. This diver's knowledge of the deep water concentrations is evident in the catch rate data (Fig. 5.9) which shows this diver regularly recorded the highest catch rates; these coincided with regular periods of deep water fishing on known aggregations.

The fishing pattern of day 3 contrasts with the initial two days, most of the initial activity being outside the central blocks and almost all the activity in the latter half of the day being inside blocks 12-15 (Fig. 5.5). However, despite this early increase in activity in the deeper blocks during day 3 the proportions of effort and catch taken in the shallow depths for the whole day were not very different to that of days 1 and 2 (Fig. 5.7a). Again diver 2 was responsible for 40% of the effort expended in the deeper areas, but the other divers, particularly diver 1, began making short short exploratory dives in different deeper parts of the research area (Fig. 5.8). This resulted in the mean time spent continuously in any single deep water block declining markedly on day 3 (Fig. 5.7c).

By contrast, the mean time spent continuously in the shallow water blocks increased and this also reflected a change in the fishing pattern of the divers in these blocks. In the first two days when the catch rates had been higher the divers were relatively unfamiliar with the area and swam rapidly, covering relatively large distances and moving between blocks. The divers call this type of activity, which combines abalone gathering with exploration, skimming, and use it to maximize the chance of finding areas with high concentrations of abalone. As catch rates declined and they became more familiar with the area, the divers became less interested in continually scanning and exploring the area and more interested in searching for abalone in a more thorough, systematic fashion.

During day 4 the proportion of effort expended in depths <10 m declined markedly as all divers concentrated more of their effort in the deeper blocks (Fig. 5.7a). The catch rates recorded in the deeper blocks increased by *c.* 20%, which caused the overall catch rate for day to increase (Fig. 5.7b). The catch rates experienced in the shallow blocks continued to decline.

The trend towards concentrating effort into the deeper blocks continued on day 5 and the mean time spent continuously in any single deep water block also continued to

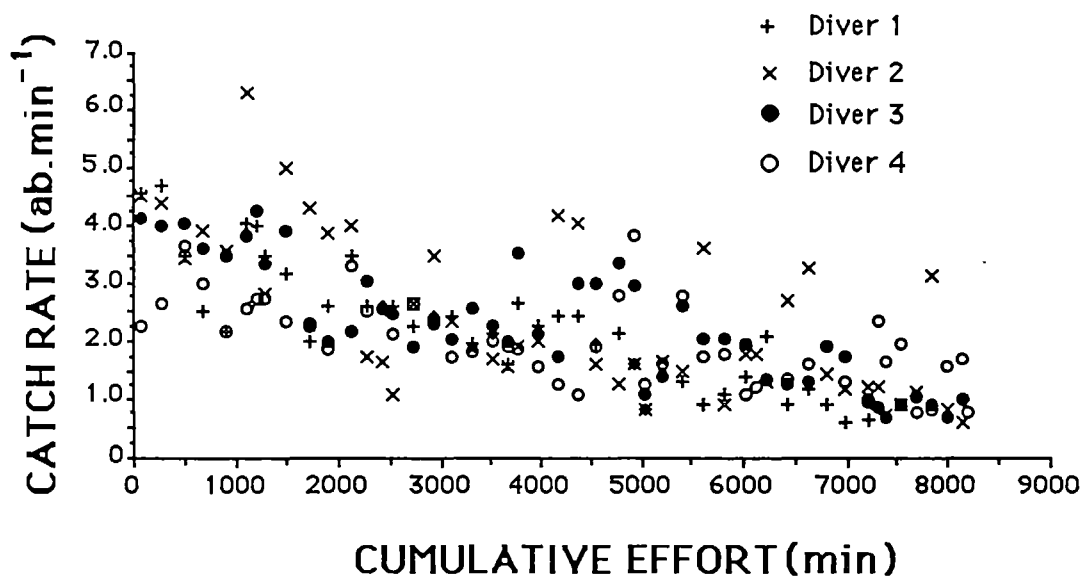


Figure 5.9
Hourly catch rates (ab.min⁻¹) of individual divers against cumulative effort (min).
expended, data for all blocks pooled.

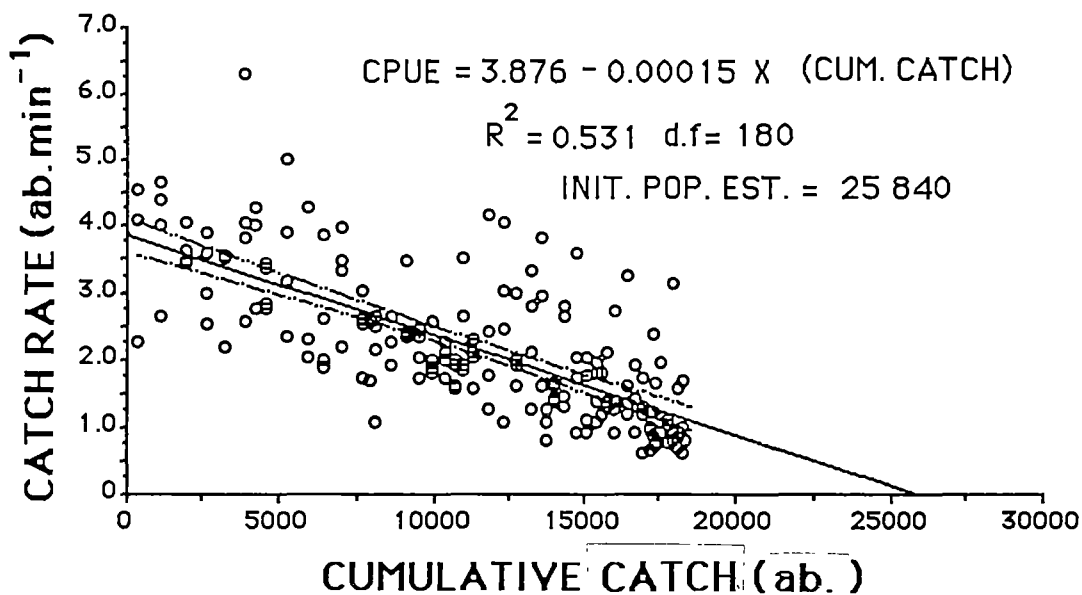


Figure 5.10
The trend in hourly catch rate (ab.min⁻¹) pooled for all blocks and divers, and
showing the fitted regression and 95% confidence limits around the regression.
The slope of the regression and x-intercept are the Leslie estimates of catchability
coefficient (q) and population size (ab) respectively.

increase. However the catch rate in the deep water blocks declined towards that in the shallow blocks (Fig. 5.7a-c). The time spent continually in shallow water blocks declined markedly on day 5 to its lowest level for the experiment, suggesting that the divers were re-assessing the catch rates available in the shallow blocks and making short exploratory dives in that area again.

During days 6 and 7 the proportion of the effort expended in the shallow areas returned to the levels of the first three days as most of the divers began allocating more of their effort to the shallow areas. The difference between the catch rates of deep and shallow water blocks returned to that observed between them during days 2 and 3. The average time spent continuously in shallow and deep blocks converged suggesting that few exploratory dives were being made in either habitats. When the catch rates declined below about 1.5 ab.min.^{-1} on the sixth and penultimate day (Fig. 5.7b) the catch rates were below the level that could be expected in commercially accessible grounds surrounding the experimental area. Consequently, the enthusiasm of the divers for the experiment began to wane over the last two days. By this time, they were also relatively familiar with the area and relatively confident that few if any concentrations of abalone remained to be found. During this period the divers seemed to settle into relatively stable fishing patterns, choosing an area and continuing to search it regardless of the result. Three of the divers concentrated virtually all their effort in the shallow water during this period explicitly stating to the observers that they considered that the low catch rates did not justify the health effects incurred by diving in the deeper water. Diver 4 chose to ignore accepted diving practices and concentrated most of his effort in the deeper areas, choosing to take advantage of the slightly higher catch rates in those blocks. This diver's daily catch had been consistently less than the other divers through the experiment, but by concentrating his effort on the deeper blocks he was able to record the highest catch on the last day.

5.3.2 Leslie Population Estimates

Using the hourly summaries of catch and effort data for individual divers, over the 7 days of fishing and pooling over all the blocks, the initial size of the population was estimated (Fig. 5.10) to be v. 25 840 abalone (95% C.I.= 22 679 – 29 976) and the catchability coefficient (q) 1.5×10^{-4} (95% C.I.= 1.3×10^{-4} – 1.7×10^{-4}). The catchability coefficient indicates that approximately 0.015% of the abalone remaining in the area at any

time were caught for each minute of diving effort or 0.9% for each hour. The research site contained approximately 360 000 m² of reef therefore the fishing power of a diver was approximately 54 m² min⁻¹. This value means that theoretically a diver could search an area of 54 m² every minute with 100% efficiency.

These estimates assume that catch per unit effort is directly related to the abundance of abalone. However it has already been noted that a considerable amount of the variability observed in these data could be attributed to factors other than abalone abundance. The fishing pattern of the divers over the 7 days of the experiment was one factor observed to influence the catch and effort data and for this reason it could be envisaged that running the experiment over varying time spans could effect the estimates of population size.

The effect of running the experiment for shorter time spans has been simulated by truncating the data set at the end of each days diving and doing the Leslie analysis with the shortened data sets (Table 5.1). No significant trend in catch rate was evident over the first day of diving. However over the next two days of fishing a significant relationship between catch rate and cumulative catch became evident. Using the data up until the end of the third day it is possible to estimate population size as 20 505 abalone and q as 2.0×10^{-4} . Overall catch rates increased on day 4 when the divers began using the deeper blocks more extensively. Correspondingly the regression coefficient for the relationship up until the end of day 4 decreases, and there is a 30% increase in the estimated population size together with a decline in the catchability coefficient. The estimates of the parameters exhibited less volatility over the last three days of the study with the estimates of population size slowly declining and the estimate of catchability slowly increasing, towards the final estimates. However, it is of interest to note that the final estimate of total population size, 25 840, is still on the lower side of the estimates produced from the tagging study 28 000 - 33 000.

Considerable variation was observed when the catch and effort data from individual divers were compared. Data for diver 1 (Fig. 5.11a) produced the lowest estimate of population size (22 124) and the highest estimate of q (1.85×10^{-4}) while those for diver 4 (Fig. 5.11d) produced the highest estimate of population size (34 710) and the lowest estimate of q (0.85×10^{-4}). Differences between divers can be explained by differences in their fishing behaviour, rather than by individual differences in diver efficiency. Diver 1 expended less effort (taking into account the fact that he did not fish on day 7) in the deep water blocks than any of the other divers (Fig. 5.8) and experienced a more severe decline in catch rates than the other divers. In contrast diver 4 concentrated a large amount of his

Figure 5.11

The trend in hourly catch rate ($\text{ab} \cdot \text{min}^{-1}$) pooled for all blocks but separated by diver (Divers 1-4 are Figs a-d respectively) showing the fitted regressions and 95% confidence limits around the regressions. The slope of the regressions and x-intercepts are Leslie estimates of catchability coefficient (q) and population size (ab) respectively.

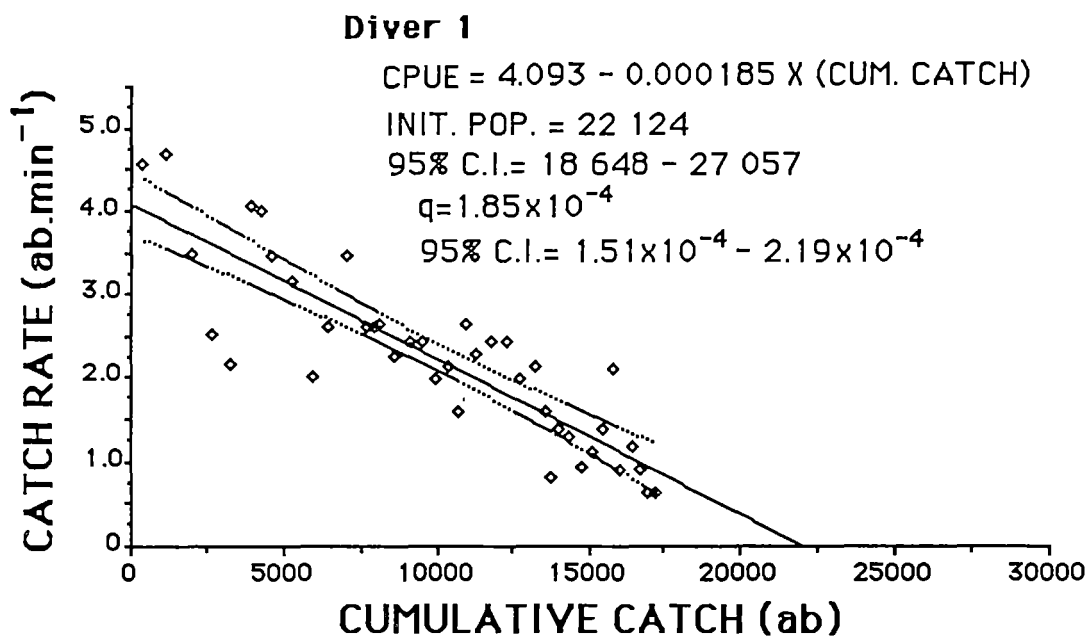


Figure 5.11a

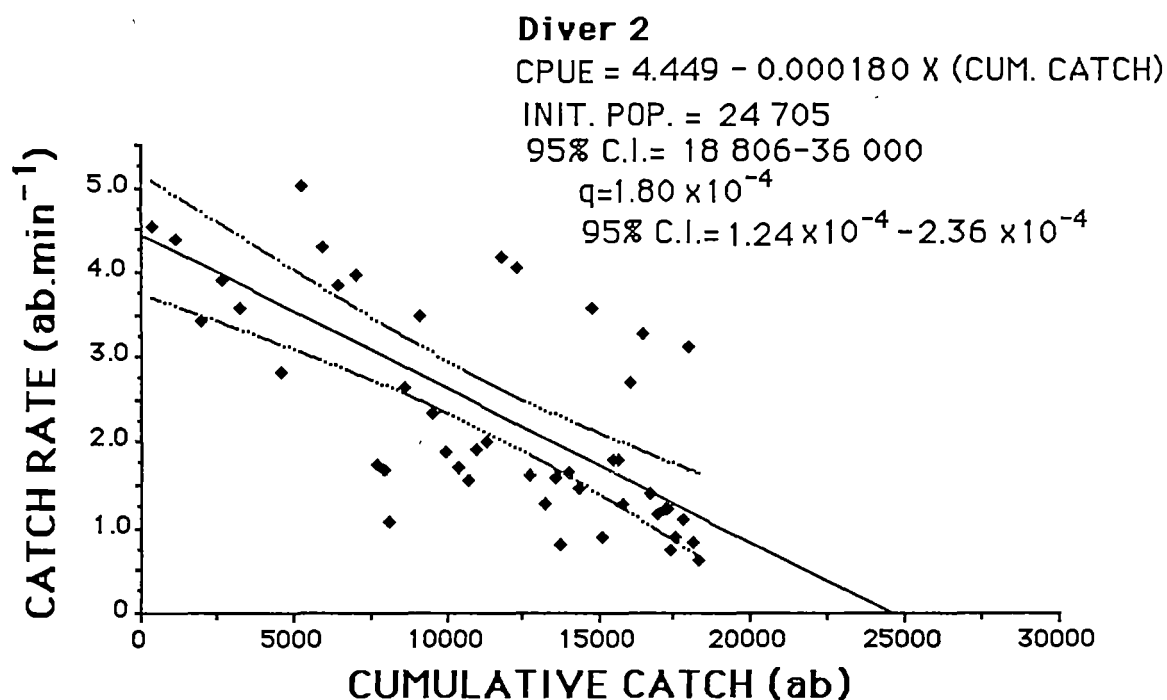
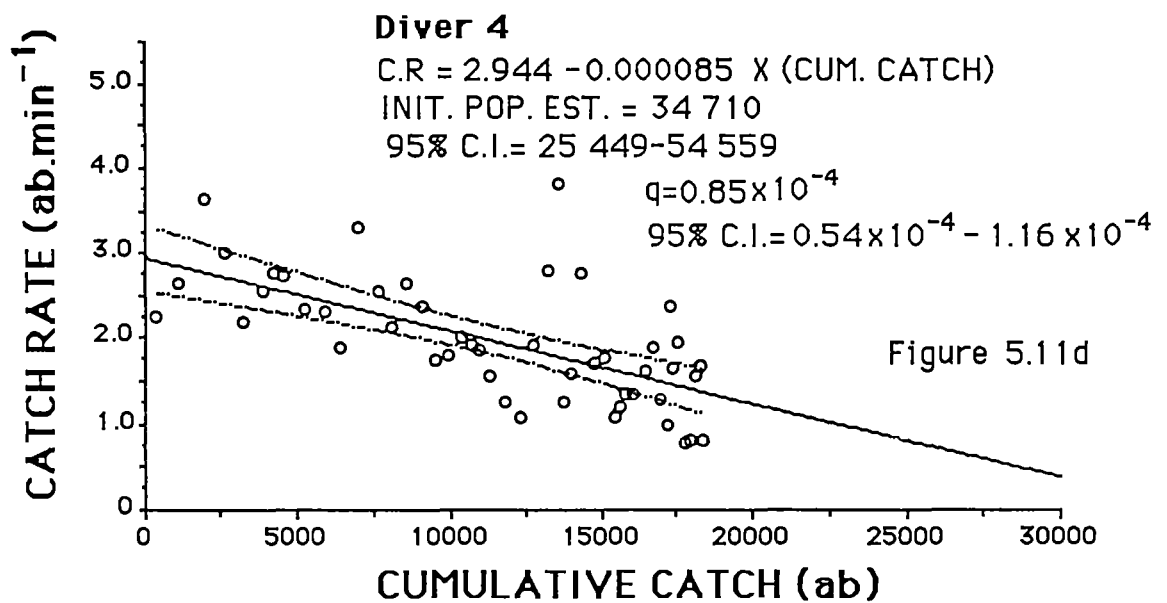
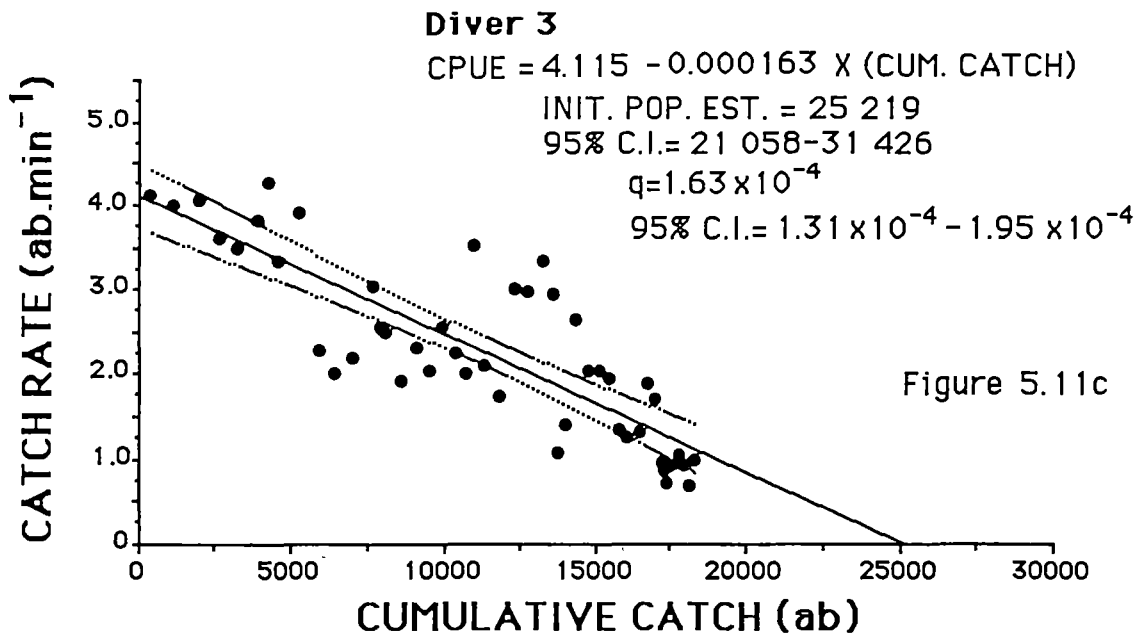


Figure 5.11b



effort in the deep water towards the end of the experiment and consequently finished the experiment with relatively high catch rates and a less severe decline in catch rates.

Table 5.1 Variation in the estimated values of population size and catchability over the duration of the fish down experiment.

Day	Population Estimate			Catchability ($\times 10^4$)			r^2	d.f.	p
	-95%		+95%	-95%		+95%			
1	-	61 901	-	-	0.61	-	<0.1	26	0.67
2	14 362	22 751	54 060	0.74	1.77	2.80	0.19	53	<0.001
3	16 194	20 505	27 788	1.47	2.00	2.53	0.42	81	<0.001
4	20 266	27 453	38 354	0.95	1.39	1.79	0.31	109	<0.001
5	21 628	26 094	32 676	1.18	1.48	1.78	0.41	135	<0.001
6	22 598	25 998	31 310	1.23	1.49	1.70	0.49	161	<0.001
7	22 679	25 840	29 976	1.29	1.50	1.71	0.53	180	<0.001

The catch and effort data can also be broken so that estimates of population size can be made for many of the individual blocks. The number of data points is limited for many blocks so it is necessary to pool the data for different divers. Figure 5.12 shows the estimates of catchability (a) and populations size (b) for those blocks where estimates were possible. Some idea of the error structure associated with these estimates is provided by the 95% confidence intervals shown for the estimates of q which is the slope of the regression equation used to make these estimates.

From these data it is evident that the central shallow blocks (12-14) had relatively high densities of abalone, with a mean of 3 847 ab.block⁻¹, and a low mean catchability (0.0012). In contrast the mean density of abalone in the deeper water blocks was almost an order of magnitude less (498 ab.block⁻¹), while the catchability was almost an order of magnitude higher (0.0090). These estimates, together with the area of each block (15 625 m²) make it possible to estimate the fishing power of a diver in the shallow and deep water blocks respectively as 18.8 and 140.6 m².min⁻¹ and the initial population densities in each habitat as 0.25 ab.m⁻² and 0.03 ab.m⁻² respectively.

The difference between these two habitats can be explained by the fact that in the deeper areas abalone are more strongly aggregated, congregating along the sand edges; while in the *Durvillaea* habitat abalone occurred relatively uniformly throughout the shallow water blocks. The divers know the preference of abalone for these sand edges

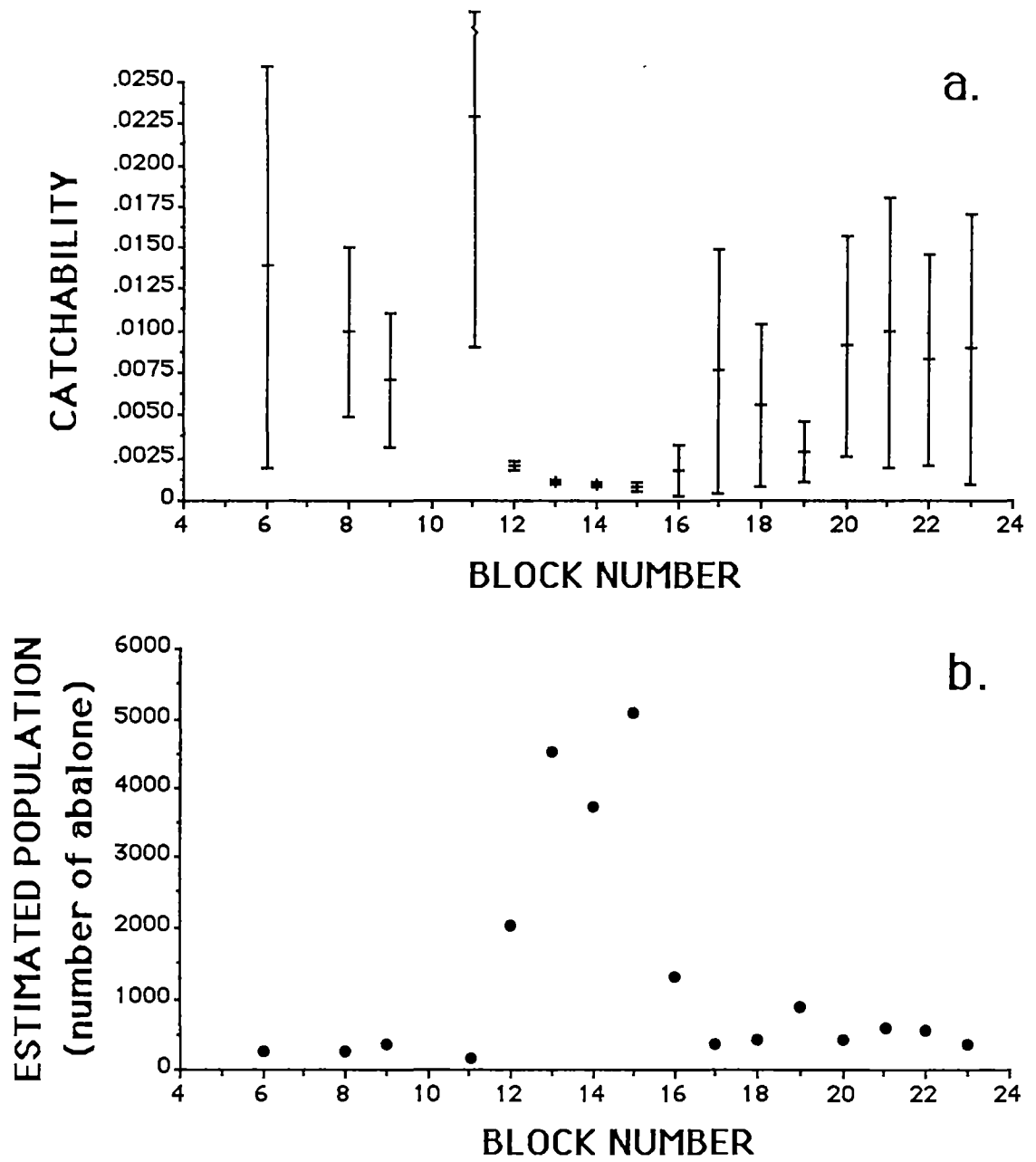


Figure 5.12
Leslie estimates of the catchability coefficients 'q' with 95% confidence intervals (a)
and population size (b) in number of abalone.

and did not search the deeper areas randomly, instead they concentrated their effort on that particular part of the deeper habitat. Thus the catchability of the abalone in the deep water habitat is greater than in the shallow.

From these estimates it is also possible to estimate that there were approximately 14 500 abalone in the shallow water blocks prior to the fish-down experiment which, depending on whether the Leslie or the tag-derived estimate (v. Chapter 4) of population size is used, was 56 or 48% of the total population respectively. Approximately 63% of the tagged abalone were released into these blocks, indicating that tagged abalone were dispersed amongst the population in a manner which reflected the population structure relatively well. This observation increases the confidence that can be placed in the tagging estimates by reducing the possibility of bias in those estimates (v. 4.4.6).

It is interesting to note that the estimate derived by this study for the fishing power of divers in the *Durvillaea* habitat which is equivalent to $1128 \text{ m}^2 \cdot \text{h}^{-1}$ agrees closely with the estimate of $1196 \text{ m}^2 \cdot \text{h}^{-1}$ that Beinssen (1979) derived for divers collecting the same species in the Victorian fishery.

5.3.3 Independent Assessments of Density

A total of 35 legal sized abalone were collected from two $15 \times 15 \text{ m}$ areas that were searched in the shallow water habitat of block 14, an approximate density of $0.08 \text{ legal sized ab. m}^{-2}$. The density measured prior to the fish-down experiment in this area was $0.39 \text{ legal sized ab. m}^{-2}$ suggesting a density reduction of 79.5 %. The population estimate for block 14 made using the Leslie technique was 3 746 legal size abalone and 2 937 were captured during the fish-down, suggesting a reduction in population of 78.4%.

5.4. CONCLUSIONS

These data illustrate the interactions between human behaviour and abalone biology, which occur on a small scale within an abalone fishery. The fishery exploits a species with highly heterogeneous distribution. The visual nature of a diver's operation, together with the relatively sedentary nature of the abalone and long term stability of their populations give the divers a high degree of knowledge about their distribution. Divers make complex decisions about their fishing patterns, weighing up expected catch rates and returns, against expected costs and comfort levels, and targeting areas of stock which they consider most desirable in the light of all the different factors. The way divers allocate their effort over the spatially heterogeneous stock produces a high degree of

variability within observed CPUE data which can obscure or bias the relationship between CPUE and actual stock abundance.

However these results also suggest that if the effect of diver behaviour and the spatial distribution of the abalone is excluded by considering small (100 x 100 m) discrete homogeneous areas, catch rate will reflect the true abundance of abalone relatively accurately.

CHAPTER 6

MODELLING THE DYNAMICS OF AN EXPLOITED STOCK OF *HALIOTIS RUBRA*.

6.1 INTRODUCTION

As a way of drawing the different facets of this study together, I have constructed a computer model of an exploited population of *Haliotis rubra*. The purpose of this model is to explore more fully the ramifications the results of this study have for the assessment and management of abalone fisheries. In particular I wish to explore the relationship between CPUE and stock abundance over an extended time scale.

When studied in isolation, different biological characteristics of an exploited species may appear likely to affect the dynamics of a species in a relatively simple way. However, when combined with other characteristics unforeseen interactions may cause the studied population to behave unpredictably. The benefit of using a computer or logic model to describe the dynamics of an exploited population is that it allows these interactions to be explored in an interactive or experimental manner.

This chapter combines the results of previous chapters, together with other published results to simulate a single population of abalone. The results used to construct this logic model have already been discussed within the various chapters of this thesis or the studies in which they were published, and it is only the manner in which they have been interpreted or used that will be discussed here. I have used some biological characteristics and parameters in a relatively speculative fashion and have tried to highlight and discuss the extent of this speculation. However the model presented here and the results drawn from it should be accepted within this context of speculation and exploration of different possible hypotheses.

6.2 DESCRIPTION OF THE MODEL

6.2.1 Physical Structure of the Modelled Reef

The model I have constructed describes the dynamics of an abalone population similar to the population studied at George III Rock (v. Chapters 4 & 5). To this end a self-contained area of reef has been envisaged that is a square made up of 25 cells, each 100 x 100 m. The central cell is envisaged as being the shallowest section of the reef, with a depth gradient existing between the central and outermost cells (Fig. 6.1).

6.2.2 General Population Structure

The model follows 15 year classes, with the oldest year class being an

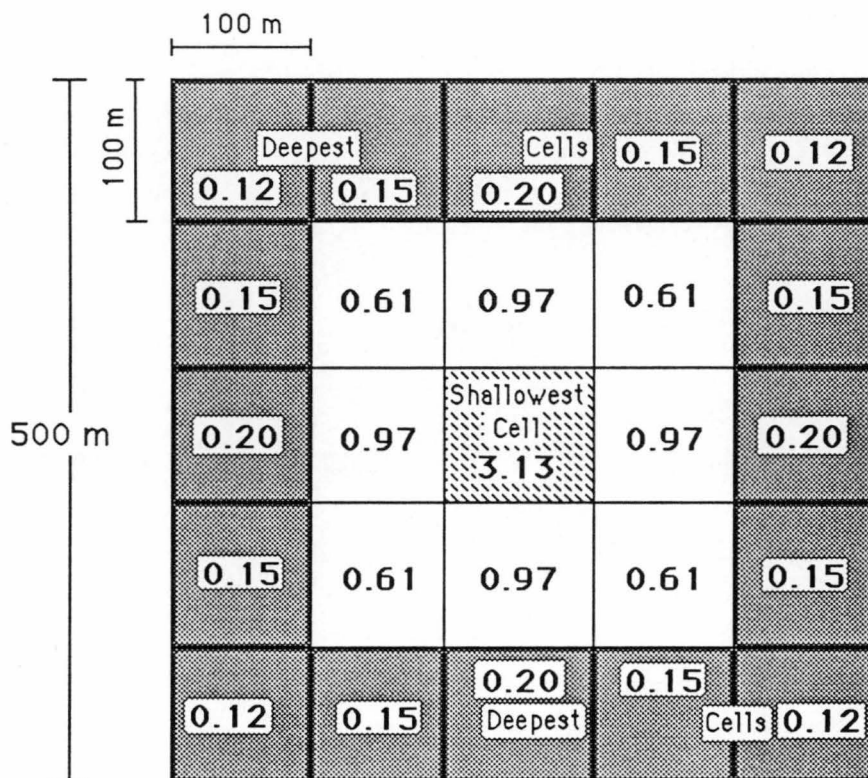


Figure 6.1

The hypothetical reef structure conceptualized for the abalone population model. The figures in bold type are tonnes of breeding stock.cell⁻¹ and indicate a typical stock distribution pattern produced by the movement parameters of the model.

accumulation of older year classes which are assumed to have the same body weight and the same mortality rates. The growth parameters used within the model are those observed at George III Rock and the model reads in directly an average weight for each year class (Table 6.1). The survivorship table (Table 6.1) used by the model is loosely based on mortality data gathered in Chapters 2 and 5 and the survival of each age class is also read in directly by the model. Mortality is assumed to decline from approximately 60% per annum in the youngest age class to 10% in the oldest age classes.

For simplicity, maturity and recruitment to the fished population is assumed to be knife-edged, with all abalone maturing and entering the fishable population during their 8th year of life (7+).

Table 6.1 The weight at age and survivorship schedule used in the abalone population model. The weight at age schedule uses the length–weight and growth parameters for the abalone population at George III Rock, while the survivorship schedule is derived from the results of Chapters 2 & 4.

Year	Weight (kg)	Survival (annum ⁻¹)
1	0.0006	0.30
2	0.0008	0.40
3	0.043	0.45
4	0.115	0.50
5	0.207	0.55
6	0.298	0.60
7	0.371	0.65
8	0.423	0.70
9	0.459	0.80
10	0.482	0.85
11	0.497	0.87
12	0.506	0.88
13	0.512	0.89
14	0.515	0.90
15	0.517	0.90

6.2.3 The Relationship between Stock and Recruitment

The two curves most commonly used to describe the relationships between the

abundance of breeding stock and subsequent recruitment are the Ricker (1954) and Beverton and Holt (1957) curves. The standard Ricker equation:

$$\text{Recruitment} = S.e^{(a-bS)} \quad \text{eq. 6.1}$$

where 'S' is the abundance of spawning stock, describes a bell shaped curve whose shape is defined by the parameters 'a' and 'b'. The Beverton-Holt equation:

$$\text{Recruitment} = a.S/(1+bS) \quad \text{eq. 6.2}$$

describes a curve which increases towards some upper value before plateauing. In this equation the parameter 'a' defines the the height of the plateau and a/b the slope of the curve.

The shape of both the Ricker and Beverton-Holt recruitment curves convey little advantage on an aggregating animal. This is because recruitment is almost directly proportional to spawning stock abundance at low densities; in other words the number of recruits produced per spawning adult remains relatively constant at low densities. The implication of this for abalone is that a number of low density patches will produce the same amount of progeny as half the number of patches with double the density.

It is clear from the literature and observations made during this study that abalone distribution is strongly clumped, and that abalone actively form these aggregations. Aggregation for breeding has been observed in *H. laevigata* by Shepherd (1986b) and suggested for many other species of abalone by other workers who hypothesised that aggregation would increase the success of broadcast spawning events. This study produced no direct evidence of aggregation for breeding, although movement out of the cryptic habitat was clearly linked with sexual maturity, and directional movements which could be responsible for the formation of observed aggregations were documented.

There is no basis for suggesting that feeding or survival are enhanced through this aggregation. However, the possibility that aggregation is not an active but a passive process, cannot be dismissed. It is possible that aggregation could occur not because it favours the abalone population but because individual abalone are all seeking similar resources. In this study there was no evidence for this type of individually beneficial directional movement, in fact directional movement was not associated with the one resource examined quantitatively, namely food, or as far as qualitative impressions could determine, to any other resource.

These factors support the accepted notion that for abalone there is an adaptive advantage in aggregating conferred through breeding. In this situation we should expect the existence of a stock-recruitment relationship which is sigmoidal at low densities of breeding stock implying that the number of recruits produced per spawner increases with increasing density. This type of curve will convey advantage on a species which actively aggregates because at low densities a single high density aggregation will produce more young than two half density aggregations. This shape at lower densities is in fact also suggested by the data collected in Chapter 3 (v. 3.3.2.e).

With both the Ricker and Beverton-Holt curves, the number of recruits produced per spawning adult decreases at higher densities, although this effect is greatest with the Ricker curve. The Ricker curve implies that at high stock densities the absolute number of recruits declines with increasing breeding stock. This describes a biological situation where at high densities recruitment is related negatively to breeding stock abundance, suggesting not just that some resource is limited but that at high densities adult stock negatively impacts on the recruitment process. The possibility for negative interaction between adult abalone and recruitment would seem relatively high when their demersal life style is considered. For example when abalone of different sizes are held in captivity at high densities the smaller animals are often smothered by larger animals. The possibility of accidental cannibalism has also been suggested by the results of feeding study of *H. roei* which found a 0+ abalone in the stomach of a larger individual (F. Wells, pers. comm.). Smaller abalone tend to inhabit crevices that are too small for larger abalone and this undoubtedly ensures that negative interactions within abalone populations are minimized at low population densities. However at high population densities negative interactions between the different size classes would become more likely.

Consequently I have designed a curve for use within the model which incorporates these two features; an inflexion at low densities and an absolute decline in recruitment abundance at higher densities. Two forms of this stock recruitment curve were used to confer different levels of productivity upon the stock. Figure 6.2a & b shows the low and high productivity curves (curve A) compared with the cohort decay line (curve B). The cohort decay line indicates the relationship between

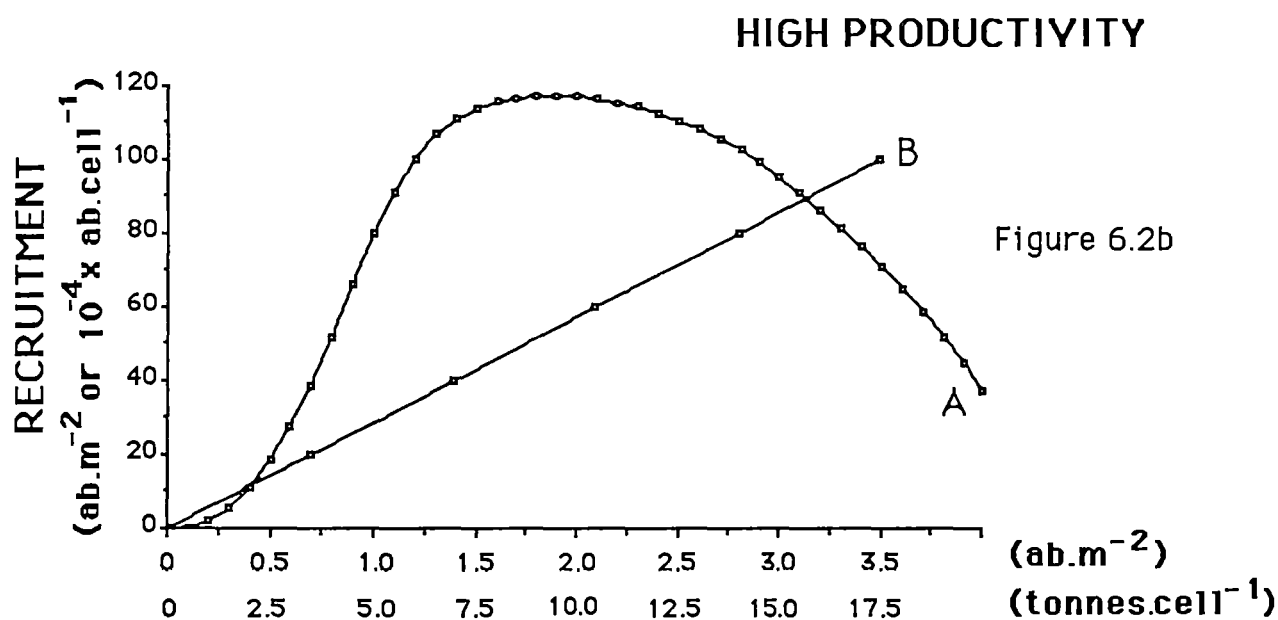
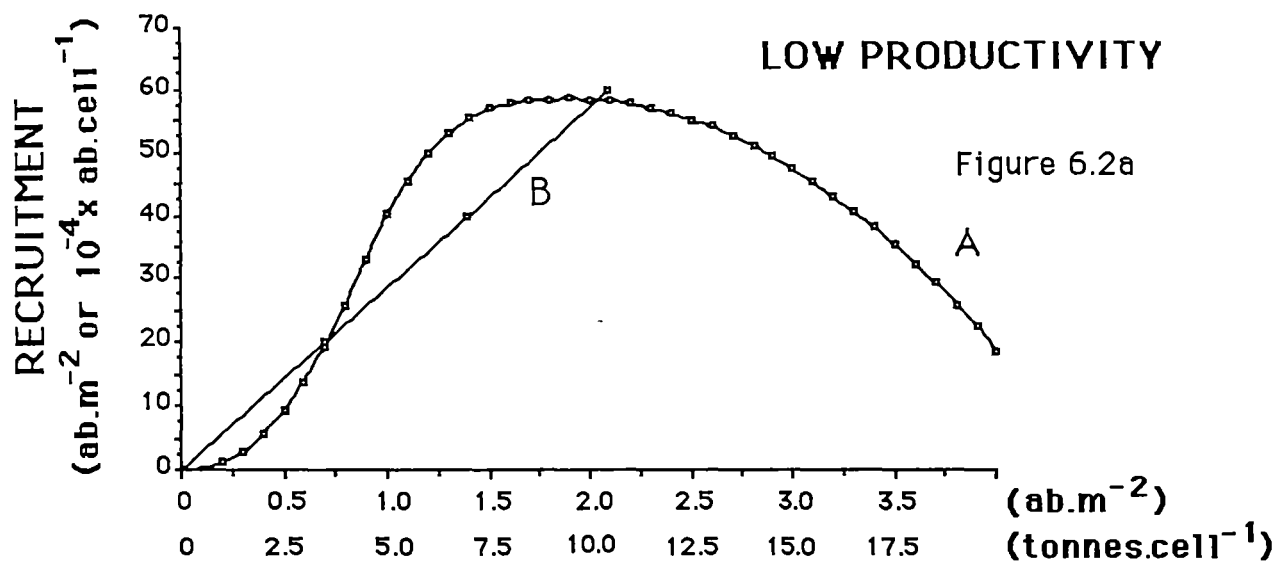


Figure 6.2

The low (a) and high (b) productivity relationships between breeding stock (tonnes.cell $^{-1}$ or ab.m^{-2}) and recruitment abundance (ab.m^{-2} or $\text{ab.} \times 10^{-4} \cdot \text{cell}^{-1}$) used for the abalone population model (curves A). Curves B in each figure show the cohort decay line (v. 6.2.3).

any constant level of recruitment and the abundance of breeding stock in an unfished population that it would produce. Where recruitment falls below the cohort decay line the stock will tend to decline towards where the two curves intersect. When recruitment is above this line stock abundance will tend to increase towards the next intersection of the curves.

I had intended using a third more productive form of this curve but found that a more productive form of this curve caused the population to cycle through extremes of low and high abundance which from the literature does not seem to be characteristic of abalone populations.

In keeping with the results presented in Chapter 3 (v. 3.4.3), recruitment is assumed to be extremely localized. The level of recruitment within each 100 x 100 m cell is assumed to be proportional to the level of spawning stock within that cell and independent of the recruitment or spawning stock in surrounding cells.

6.2.4 Movement

For simplicity, movement has been assumed to only occur amongst the mature population and to be independent of age or size amongst these animals. The directional movement of abalone has been modelled with a simple diffusion model similar to that described in Chapter 4 (v. 4.3.2.b.a). The basal annual rate of diffusion in any direction has been assumed to be 0.24 implying that during any year 24% of the abalone in any 100 x 100 m cell will move out of the cell in one of the four cardinal directions. This was slightly higher than the highest rates of movement observed at George III Rock which were oblique movements towards shallower depths in the *Durvillaea* habitat (v. 4.3.2.d). However because these movements were oblique I have assumed that the rate of movement directly towards shallow water would have been greater than measured. Within the model, this rate is assumed to be the maximum rate of movement possible. Movements that are depth neutral or negative are weighted with a movement index so that:

$$\text{Number Moving} = \text{Number in Cell} \times \text{Movement Index} \times 0.24 \quad \text{eq. 6.3}$$

At George III Rock movement was observed to be dependent upon habitat with movement being least in the habitat with an abundance of the preferred food (v. 4.3.3.c). Consequently, it is hypothesised that food availability could provide

a mechanism by which the rate of movement is directly related to population density (v. 4.4.5). This has been assumed in this model and the movement index has been made proportional to breeding stock density.

$$\text{Movement Index} = 0.239 + (0.106 \times \text{Breeding Stock Abundance}) \text{ eq. 6.4}$$

Within the model the movement index is only allowed a maximal value of 1.0 (Fig. 6.3). This index means that at high stock abundance the rate of movement towards greater depths will equal the rate of movement towards shallower depths, so that there is effectively no tendency to aggregate. In contrast, as stock abundance declines the rate of movement towards the deeper cells will decline and the relative importance of movement towards the shallow cells will increase, increasing the tendency towards aggregation.

The movement index is scaled (hence the otherwise arbitrary values of 0.24 and 0.11) so that it reaches its greatest value at the level of breeding stock which maximizes recruitment to the stock. The implication of this scaling is that when stock abundance increases to the extent that the number of recruits produced per spawning abalone declines, the stock has no tendency towards further aggregation. Without this scaling of the index, the modelled population continues to aggregate in the shallow area despite the fact that the recruit/spawner ratio declines and this leads to an eventual collapse of the population even if it is unexploited. Alternatively, the tendency towards dispersion prevents the population from reaching its full reproductive potential until a uniform density has been established in every cell.

These movement parameters cause the model to establish a density gradient over the cells at all but the highest densities, with the central cell having the highest density (Fig. 6.1). There is no provision for diagonal movement between cells and upward movements are not possible from corner cells which increases the patchiness of the density pattern and brings the model closer to reality.

The model has a minimum spatial resolution of 100 x 100 m and this prevents the description of aggregations below this scale. In the situation where the abundance of spawning stock in the central cell falls below the lower intersection with the cohort decay line (Fig. 6.2) this would make any recovery of the stock impossible since the stock continues to decline towards the cohort decay curve. To circumvent this situation, and to give the population the ability to increase from any level of

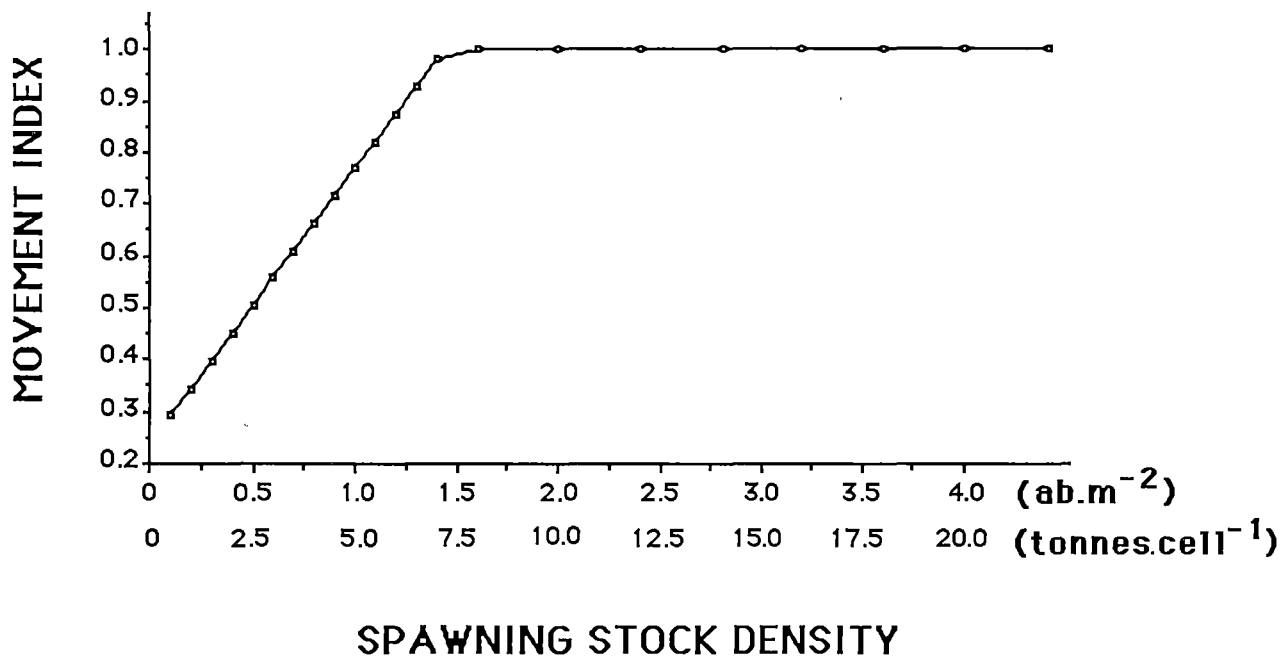


Figure 6.3 The relationship between the movement index and spawning stock abundance (tonnes.cell^{-1} or ab.m^{-2}) used in the abalone population model.

abundance, the model was been modified with respect to the stock–recruitment relationship of the central cell. At low stock abundance the stock in the central cell is assumed to collapse into an area smaller than 100 x 100 so as to achieve a density that will maximize the recruit/spawner ratio and the abundance of recruitment is estimated on the basis of the area occupied by the stock.

6.2.5 Fishery Dynamics

The relationship between catch and effort has been described with the equation:

$$CPUE = d P / (1 + h d P) \quad \text{eq. 6.5}$$

where CPUE is the catch rate of abalone in numbers per diving hour, d the density of abalone numbers per square meter, P is the fishing power of the divers in square meters effectively swept per hour and h is the handling time required to capture. The fishing power of divers, $1128 \text{ m}^2 \cdot \text{h}^{-1}$, measured in the shallow water habitat during the fish-down experiment has been used (v 5.3.2). The handling time of $5.1 \text{ sec} \cdot \text{ab}^{-1}$ measured by Beinssen (1979) has also been used. The effect of handling time is that the functional response of catch to effort expended is flattened (Fig. 6.4) at densities $>1.5 \text{ ab} \cdot \text{m}^{-2}$, or equivalent to catch rates of approximately $250 \text{ kg} \cdot \text{h}^{-1}$. However within each $100 \times 100 \text{ m}$ cell at stock densities $<1.5 \text{ ab} \cdot \text{m}^{-2}$ a close relationship should exist between catch rate and stock abundance as observed during the fish-down experiment (v. 5.3.3).

From the results obtained during the fish-down experiment (v. 5.3.1) it is clear that divers did not allocate their effort randomly. Within this model it is assumed that divers direct each unit of effort to the most preferable cell. Within the model this is achieved by using an index of preference which can be based on any number of factors to which a numerical weighting can be assigned. Two factors have been used in the model, the primary factor within the model is the abundance of abalone, however the abundance factor has been multiplied by a secondary value which is used to represent the attractiveness of shallower areas compared to deeper areas (the central cell being the shallowest and the outer cells the deepest). During the fish down experiment a consistent catch rate difference of $0.5\text{--}1.0 \text{ ab} \cdot \text{min}^{-1}$ was observed across the depth spectrum (v. 5.3.1) and the weighting factor used in this model has been scaled to maintain a difference of approximately this magnitude.

The structure of the model is such that the model assesses the relative attractiveness of each of the 25 cells before allocating a block of effort (5 h). After

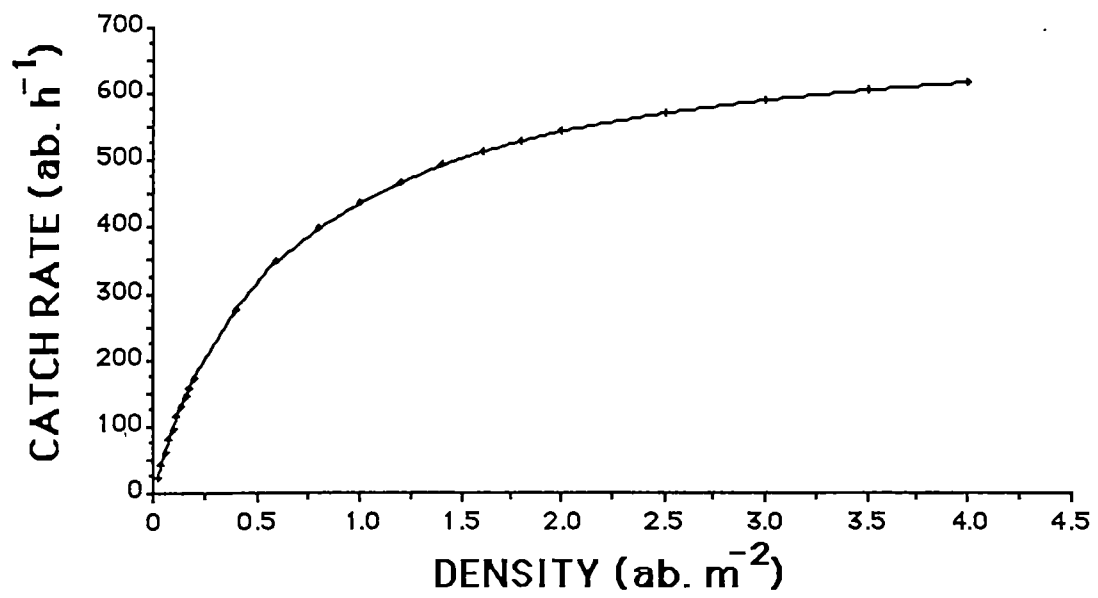


Figure 6.4
The functional response of catch rate (ab.h⁻¹) to stock abundance (ab.m⁻²)
used in the abalone population model.

allocating the effort to the most attractive cell the model estimates the effect of that effort and re-assesses the relative merits of each cell before allocating the next unit of effort.

A listing of the model in Microsoft Basic is contained in Appendix 4.

6.3 SIMULATING OF THE FISH-DOWN EXPERIMENT

6.3.1 Simulation Using a High Density Stock

The basic model described above was used to simulate the fish-down experiment described in Chapter 5 by concentrating on the fishing dynamics within a single one year loop and consequently without the compounding effects of mortality, recruitment or movement. This simulation allows the effect of handling time, and the selective allocation of effort, on the relationship between catch rate and stock abundance to be examined in more detail.

For this simulation an initial equal allocation of stock was made to each block and movement was modelled over a 10 year period before the fish-down experiment was conducted. This allowed the density pattern of the abalone to change from the initial uniform allocation to an aggregated, patchy distribution determined by the movement model. Figures 6.5a & b show the simulated fish-down performed on an estimated population of 225 000 legal sized abalone or a theoretical density of 0.9 legal sized ab.m⁻². In the simulation used to derive Fig. 6.5a effort was allocated strictly on the basis of where the best catch rate could be obtained. In Fig. 6.5b the attractiveness of different blocks was used to weight the expected catch rate. It is evident that the introduction of preference does not affect the relationship between catch rate and stock abundance, but only serves to increase the amount of variability about the curve. It is also obvious that the curve is not strictly linear. Nor does the relationship pass through the origin exactly, but exhibits a small degree of hyperstability, suggesting that a small positive catch rate is possible at a stock level of zero. Consequently in contrast to the observations presented in Chapter 5 (v. 5.3.2), population estimates made from the simulated fish-down experiment could be expected to over estimate the actual population size.

The departure from a strictly linear relationship is due to the combined effects of handling time and non-random allocation of effort. Figure 6.6a shows a simulated fish-down experiment where effort is allocated equally over the cells and

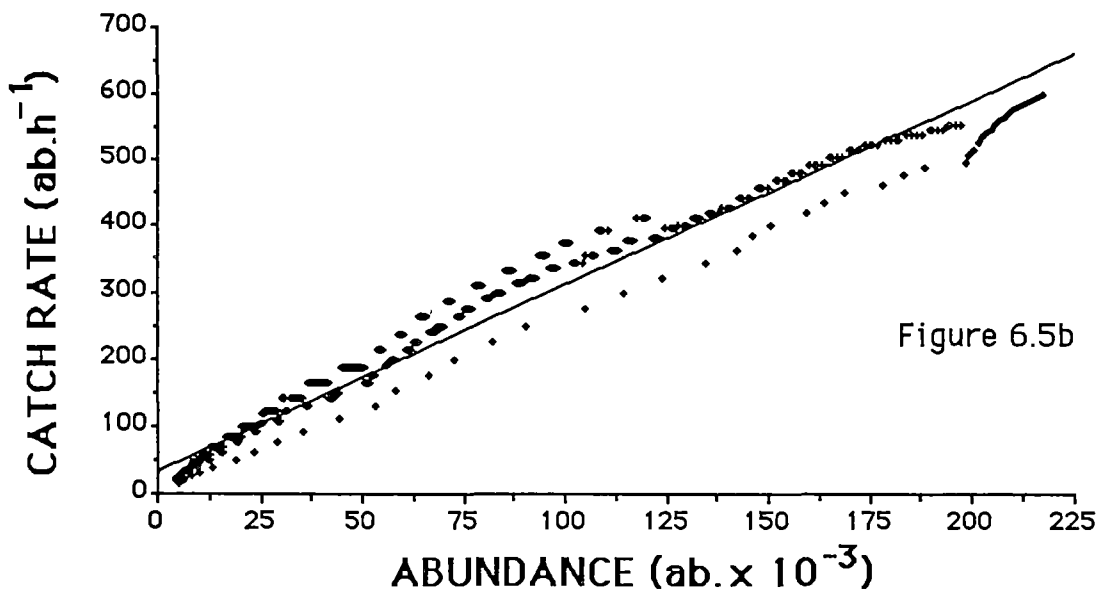
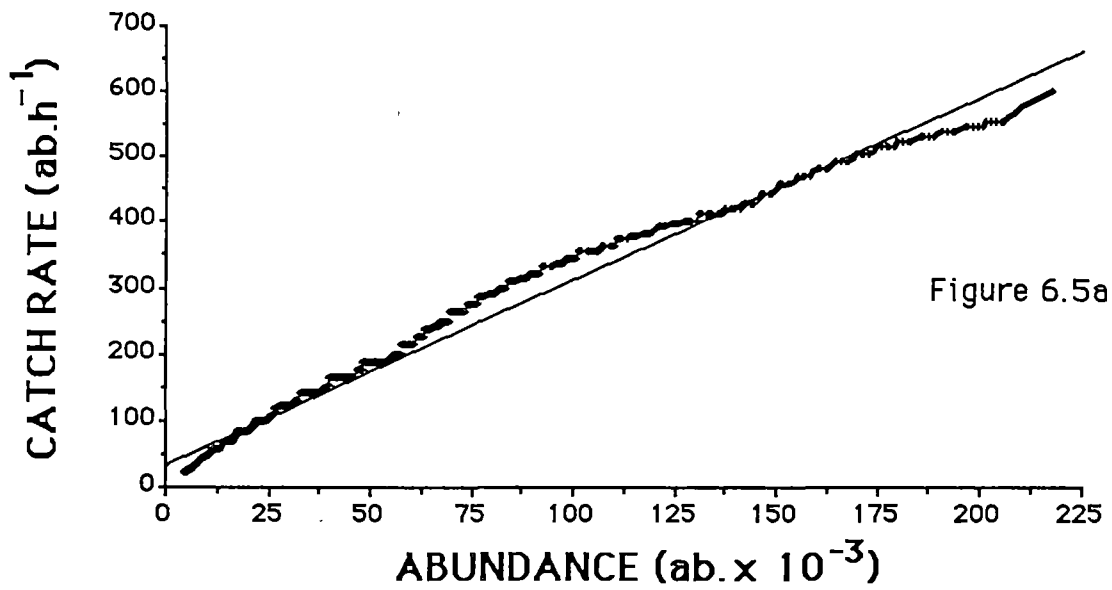


Figure 6.5

Simulated fishdown experiment performed with the abalone population model, on a population with a high initial density (225 000 abalone), effort was allocated purely on the basis of the best catch rate (a) and then allowing a depth related preference for cells (b).

Figure 6.6

Repeated simulations of the fishdown experiment depicted in Fig. 6.5 but showing the effect of: allocating effort to cells without regard to stock density or depth preference (a); assuming a linear functional response between catch rate and stock abundance (b: handling time=zero); and both of the above combined (c).

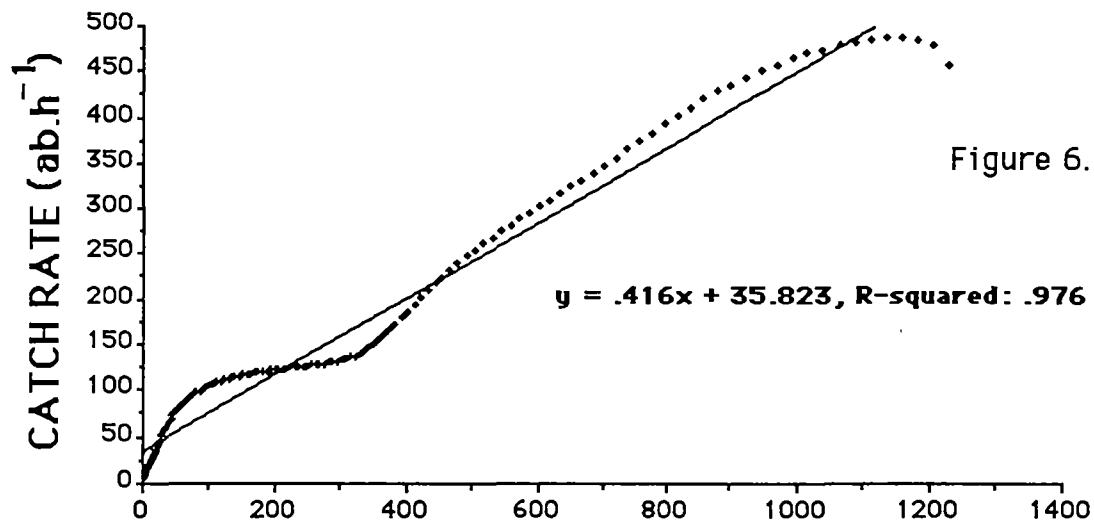


Figure 6.6a

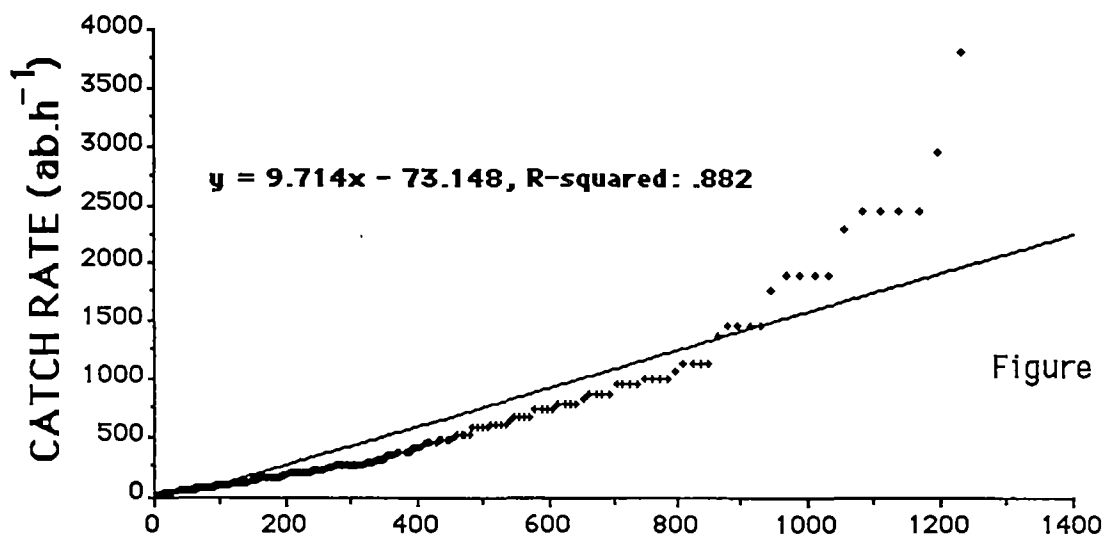


Figure 6.6b

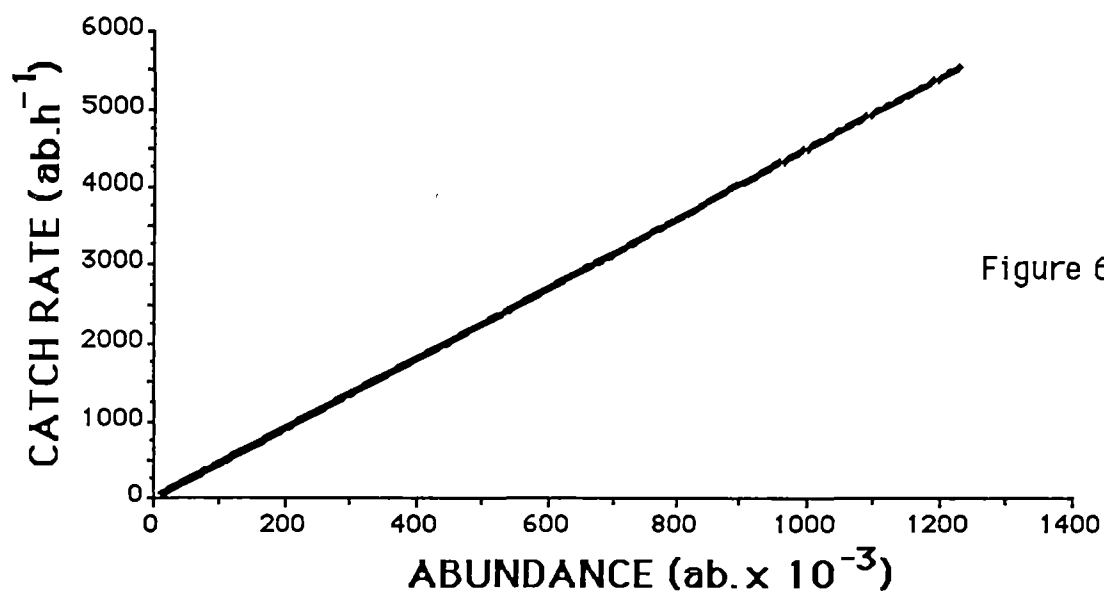


Figure 6.6c

independently to stock density or differential attractiveness of individual cells. It can be seen that quite a complex non-linear, and slightly hyperstable relationship results purely from the affect of handling time and the heterogeneous distribution of abalone over the cells. Similarly when effort is allocated on the basis of catch rate and the attractiveness of different cells but without taking handling time into account a non-linear relationship is also observed (Fig. 6.6b). However in this simulation if fishing down process was ended before the stock size was greatly reduced hyperdepletion would be observed, with catch rate declining more rapidly than stock size.

The relationship between catch rate and stock abundance is only strictly linear if effort is allocated independently of stock density and the relative merits of different cells (i.e. equally to each block) and handling time is not included in the fishery model (Fig. 6.6c).

These simulations suggest that, with regards to the relationship between stock abundance and catch rate, the effect of including handling time in the model is opposite to the effect of assuming that effort is not allocated randomly. Handling time causes the relationship to be slightly hyperstable, while targeting effort causes hyperdepletion. The opposing effects of handling time and the non-random allocation of effort in a spatially heterogeneous fish stock have already been noted by Hilborn and Walters (1987). These simulations also suggest that a fish-down experiment such as that described in Chapter 5 will over-estimate stock size. This is in contrast to the actual results of that experiment (v. 5.3.2), which together with the results of the tagging study (v. 4.4.3), indicate that the fish-down experiment actually underestimated population size.

6.3.2 Simulation Using a Low Density Stock

If the fish-down experiment is simulated with an initial stock size of only 50 000 abalone or 0.2 legal sized ab.m⁻², a different scenario becomes apparent (Figs. 6.7a & b). The relationship between catch rate and stock abundance is now similar to that observed when handling time is assumed to be zero (Fig. 6.6b) and suggests a degree of hyperdepletion. A dominating feature of this simulation is the initial rapid decline of catch rates caused by divers targeting the central concentrations of abalone. This was present in the simulation using a higher initial

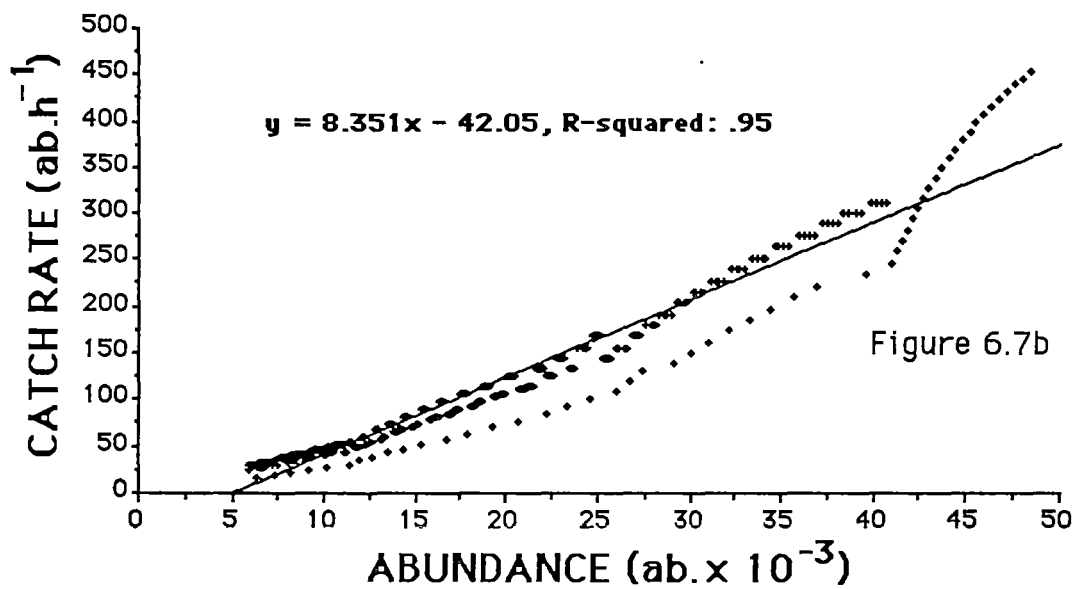
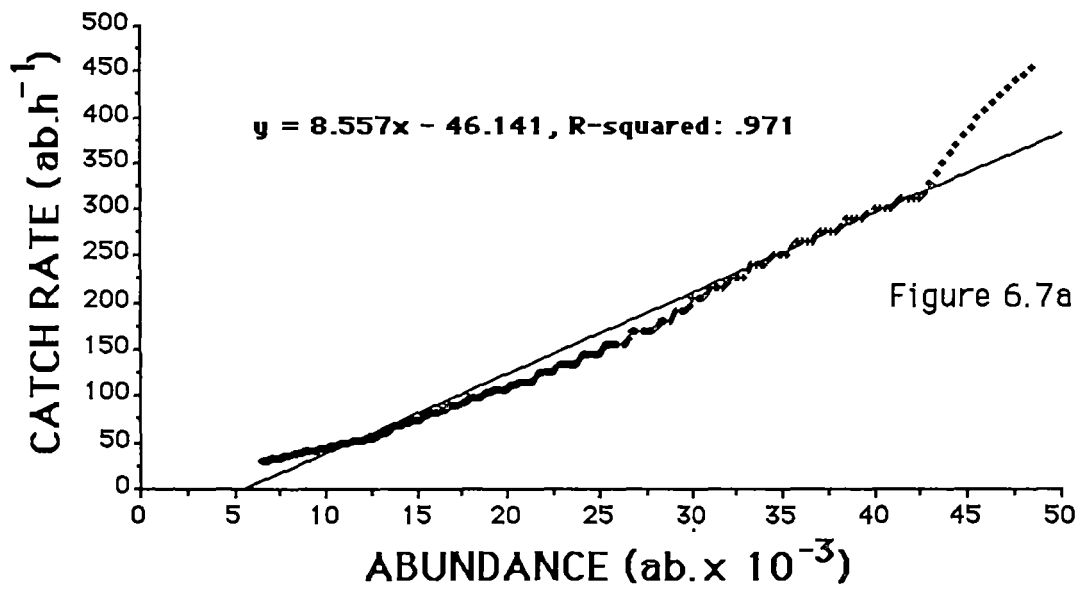


Figure 6.7

Simulated fishdown experiment performed on a population with a low initial density (50 000 abalone), effort has been allocated purely on the basis of the best catch rate (a) and also in relation to depth preferences (b).

stock abundance (Figs. 6.5a & b) but was far less marked.

It is evident that the initial decline in catch rates can be expected to produce population estimates lower than the true population. Moreover the magnitude of this bias will be related to the extent to which the original population is fished down, decreasing as the catch approaches the size of the total population. This is similar to the situation observed in Chapter 5 (v. Table 5.1) where the population estimates derived using the data from the first 2-3 days fishing produced population estimates approximately 20% below the final estimates.

6.4 SIMULATING AN EXPLOITED STOCK

6.4.1 Productivity

The model, incorporating handling time and the selective application of effort, was used to simulate the fishing of the modelled area with a constant level of effort over the time span of many years. When no fishing effort was applied the version of the model with the stock-recruitment curve conferring low productivity stabilized the spawning stock at approximately 250 tonnes and recruitment of approximately 584 000 (0+) recruits per cell. The version with higher productivity stabilized with a total spawning stock of approximately 388 tonnes and recruitment of 910 000 (0+) recruits per cell. Consequently the model was initialized with uniform introductions of stock at these levels of recruitment. As in the previous segment of the study the model was allowed to simulate the population for 10 years before exploitation was initiated, although in this case where the population was initiated at a level approaching the unfished equilibrium, the distribution pattern would have been unlikely to alter significantly during this period.

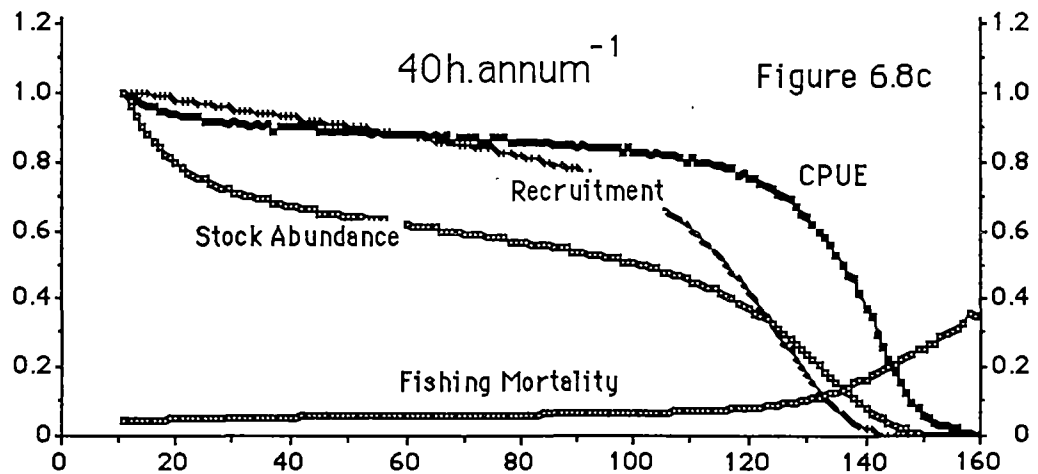
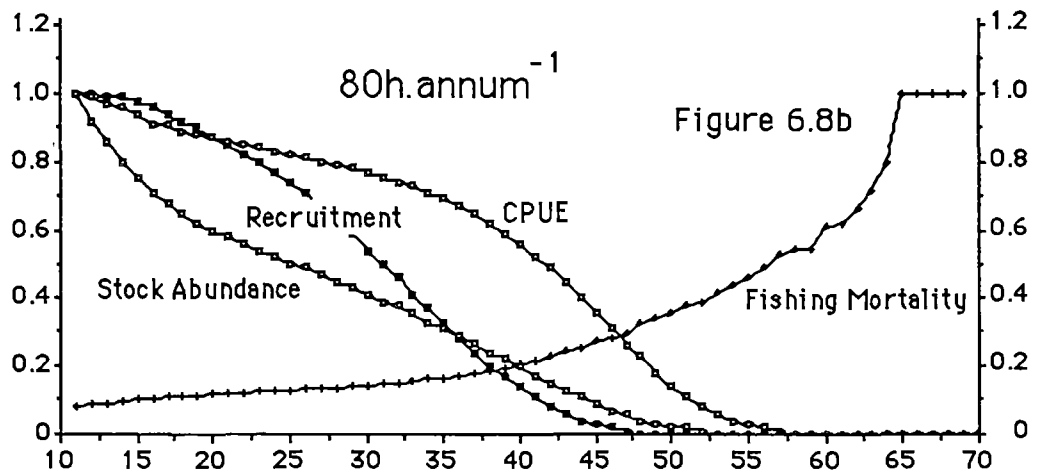
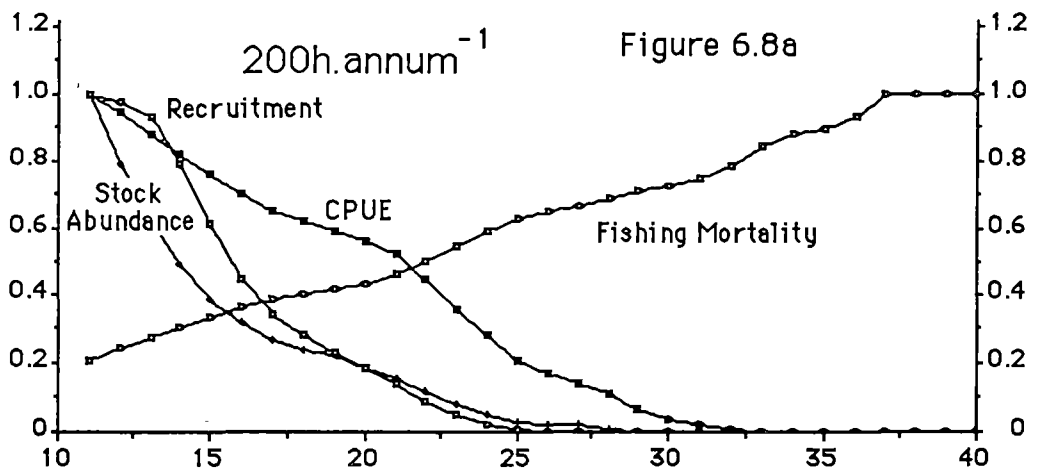
6.4.2 Dynamics of an Overexploited Stock

A range of constant levels of effort were tested with each version of the model. Figures 6.8 & 6.9 show some examples of the dynamics exhibited by each version of the model under a range of exploitation rates which eventually lead to collapse. In these figures the plotted values for recruitment denotes the relative level of recruitment into the youngest year class, and stock abundance is the level of stock resulting from recruitment to the fished population, natural mortality and fishing

Figure 6.8

Simulated exploitation of the low productivity stock (Fig. 6.2a) with a constant effort level of 200 (a), 80 (b) and 55 h.annum⁻¹ (c) showing trends in recruitment, CPUE, stock abundance (all in scaled units) and fishing mortality (proportion of available biomass being caught each year).

SCALED MEASURES OF RECRUITMENT, CPUE
AND STOCK ABUNDANCE



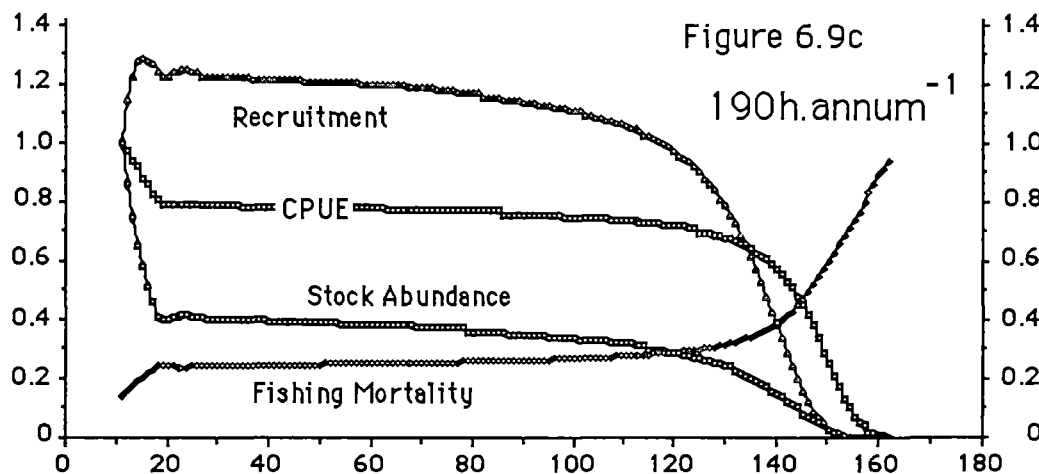
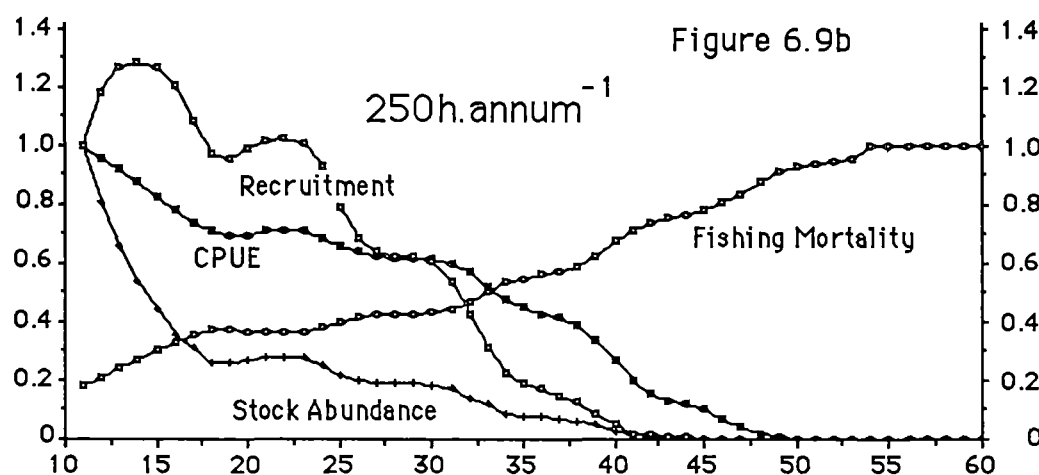
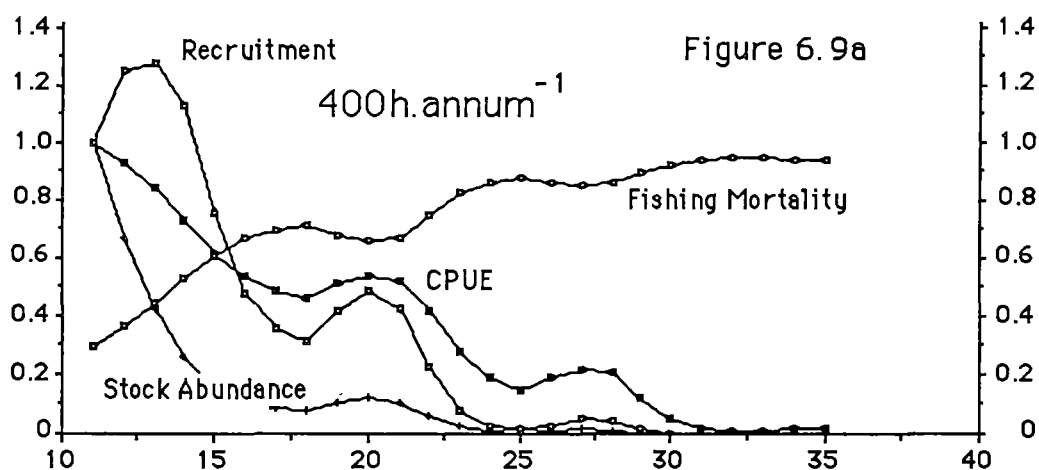
YEARS

FISHING MORTALITY

Figure 6.9

Simulated exploitation of the high productivity stock (Fig. 6.2b) with a constant effort level of 400 (a), 300 (b) and 250 h.annum⁻¹ (c) showing trends in recruitment, CPUE, stock abundance (all in scaled units) and fishing mortality (proportion of available biomass being caught each year).

SCALED MEASURES OF RECRUITMENT, CPUE
AND STOCK ABUNDANCE



YEARS

FISHING MORTALITY

mortality. The plotted value for fishing mortality is the proportion of the available stock removed by fishing. With the exception of fishing mortality, all values have been scaled in order to facilitate graphing.

While the level of effort applied clearly determines the speed with which the stock declines, a pattern is evident through the different scenarios. The first phase of these declines is clearly the fishing down phase which concentrates on accumulated virgin stock. During this period stock abundance and CPUE decline rapidly, although the decline in CPUE is much less than the decline in abundance.

The effect of the different levels of productivity is most clearly manifested at this stage of the fishery. The more productive and dome shaped stock–recruitment curve produces significantly improved recruitment as a consequence of fishing down the virgin biomass. This improvement in recruitment stabilizes stock size to a certain degree, which in turn stabilizes CPUE. Fishing mortality also stabilizes during this second phase. The duration of this phase, and its absolute level of stability, are determined by the level of effort applied; however the effect of declining recruitment eventually (age of recruitment is 8 years old) leads to a decline in stock abundance which in turn impacts upon recruitment. Recruitment failure accelerates the decline in stock abundance and eventually CPUE begins to decline; however this 'index of stock abundance' responds sometime after the 'actual stock' has begun responding to the excessive level of effort. Fishing mortality escalates rapidly during this final phase of the fishery.

In contrast to the higher productivity stock, when the lower productivity curve is used fishing down the original biomass does not improve recruitment to any significant extent. Consequently, the decline in stock and recruitment, and steadily increasing fishing mortality which characterises the initial stage of the fishery, continues unabated until the final collapse.

The model was allowed to iterate 200 years of exploitation for a range of different exploitation rates and the total production was averaged to estimate an annual production for each level of exploitation. From Figs. 6.10a & b it can be seen that the optimal level of exploitation for the low productivity stock was approximately 35 h.annum^{-1} which would have yielded approximately 8 tonnes per annum, while the optimal level for the highly productive stock was approximately 180 h.annum^{-1} for 42 tonnes. Both these levels of production suggest that the stocks are extremely

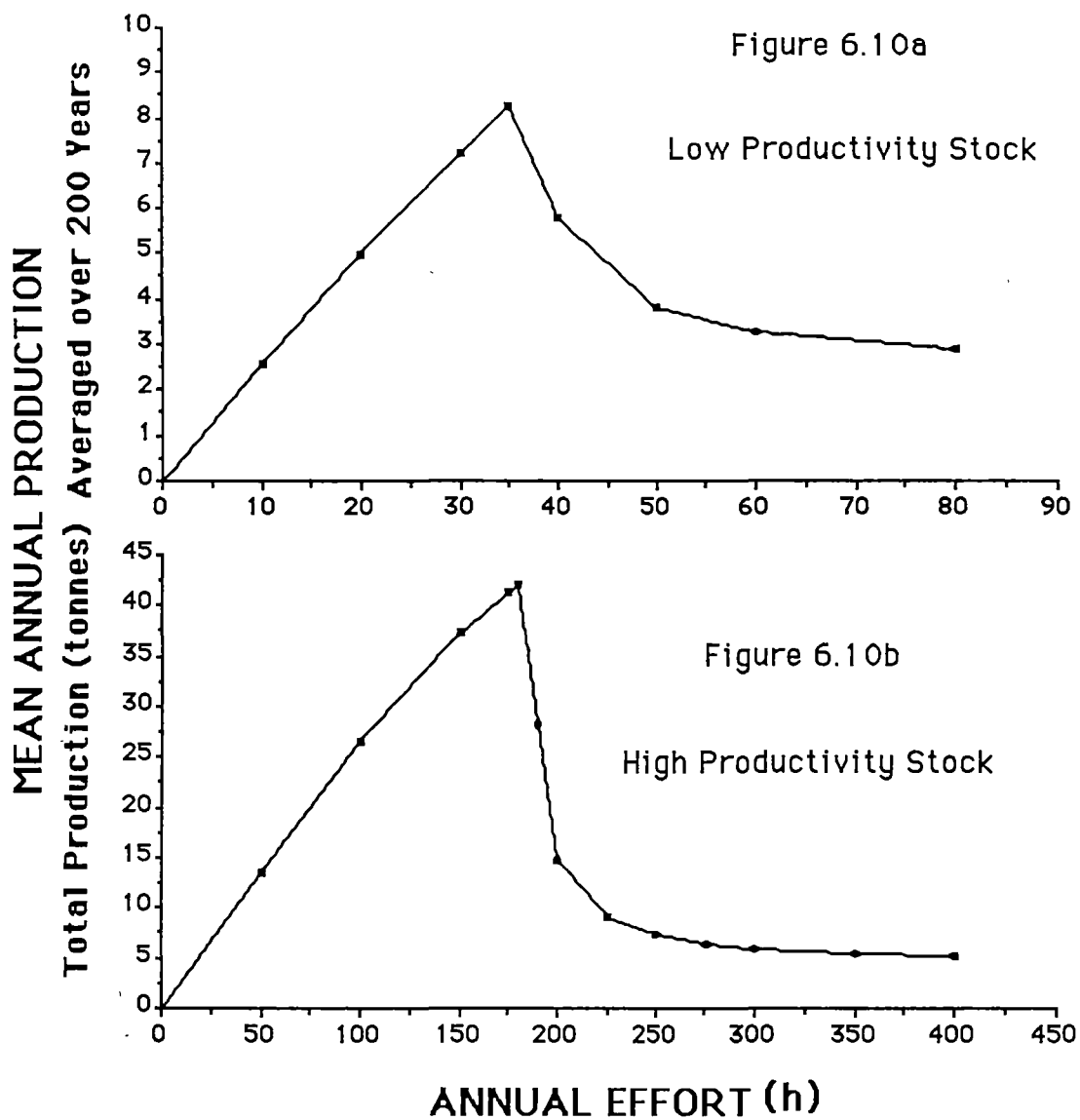


Figure 6.10
Mean annual production (tonnes) averaged over 200 y of exploitation against varying levels of exploitation ($\text{h} \cdot \text{annum}^{-1}$) for the low (a) and high (b) productivity stocks.

unproductive with the sustainable yield being 3-11% of the virgin biomass. However little can be inferred from these observations as the productivity of these hypothetical stocks is directly conferred by the stock-recruitment curves which have been assumed for the sake of this model.

6.4.3 CPUE, Stock Abundance and Fishing Mortality

From Figs. 6.9 and 6.10 it can be seen that the model suggests a degree of hyperstability with CPUE declining more slowly than actual stock abundance and stabilizing at a level that masks the actual decline in abundance. For a range of exploitation rates I estimated an expected CPUE on the basis of direct proportionality between stock abundance and CPUE. I compared this with the CPUE observed by the model, using the mean square difference between observed and expected values. Figure 6.11 shows the mean difference between expected and observed CPUE as a function of exploitation rate. From this figure it can be seen that the model predicts that, regardless of the productivity of the stock, CPUE becomes less useful as an index of abundance as exploitation rate approaches a sustainable level of fishing.

Another notable feature of Figs. 6.9 & 6.10 is the way fishing mortality escalates with time. Theoretically fishing mortality (F) should be directly proportional to the level of effort (Sands & Morgan 1976; Rothschild 1977) such that:

$$F = q \times f \quad \text{eq. 6.6}$$

where 'q' is the catchability and 'f' is the level of effort. Hence, in a stock that is fished with a constant level of effort a fixed level of fishing mortality is expected. In contrast to the expected scenario this model indicates that while fishing mortality is related to the level of effort (Fig. 6.12) it is also inversely related to stock abundance. Because these scenarios used fixed levels of effort it is apparent from equation 6.6 that the catchability (q) of the abalone increases with declining stock abundance.

At high stock densities (>1.0 ab.m⁻²) this could be attributed to the effect of handling time with an increasing proportion of effort being expended on searching as density declines, and less on handling the catch. However below this density the functional response of CPUE to stock abundance is relatively direct (v. Fig. 6.4) and the increase in catchability is attributable to the aggregative nature of the abalone, and the ability of the divers to target these aggregations. As stock

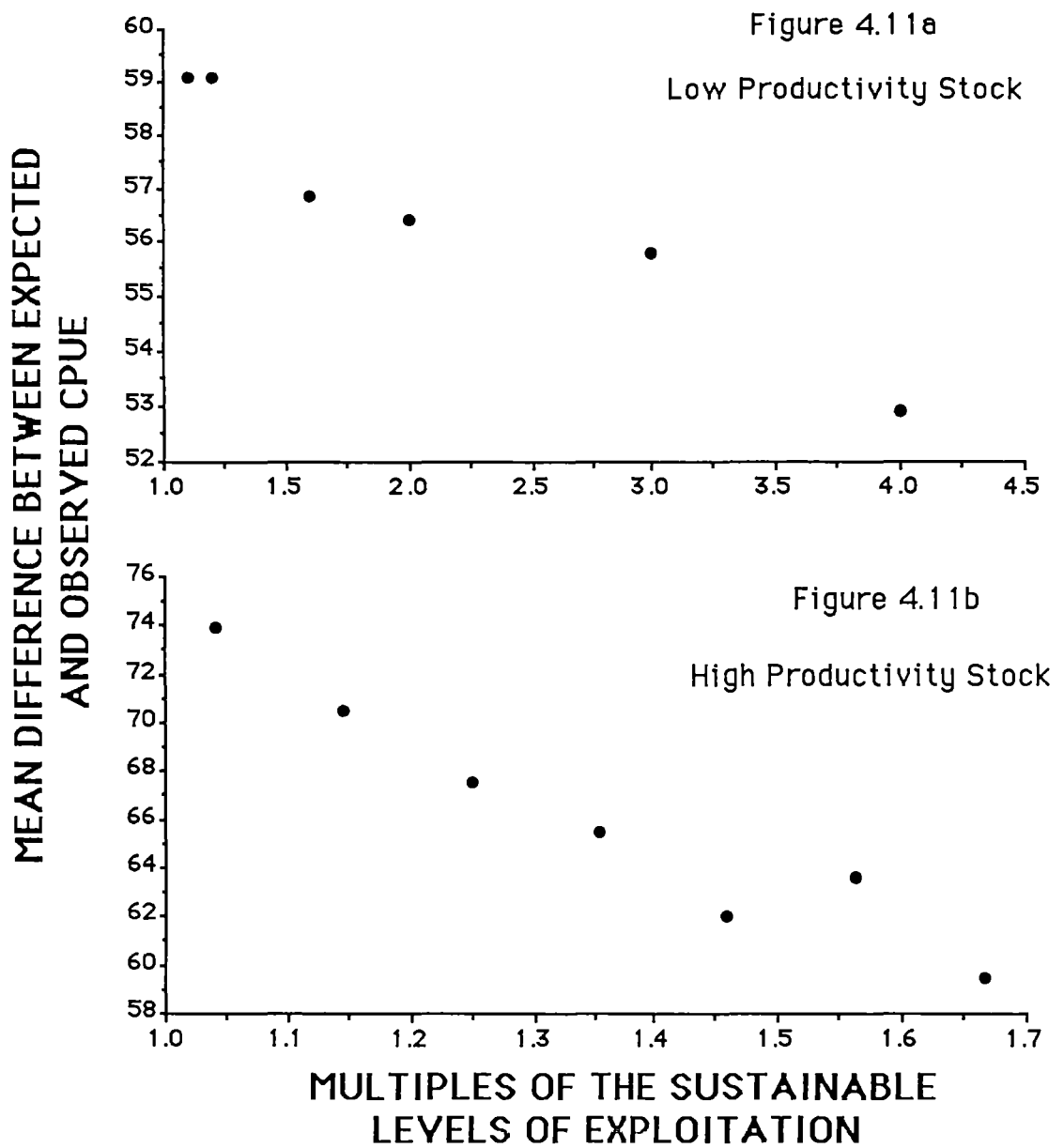


Figure 6.11
Variation in the mean difference between expected and observed catch rates with different levels of exploitation (multiples of the sustainable level of effort) for both the low (a) and high (b) productivity stocks.

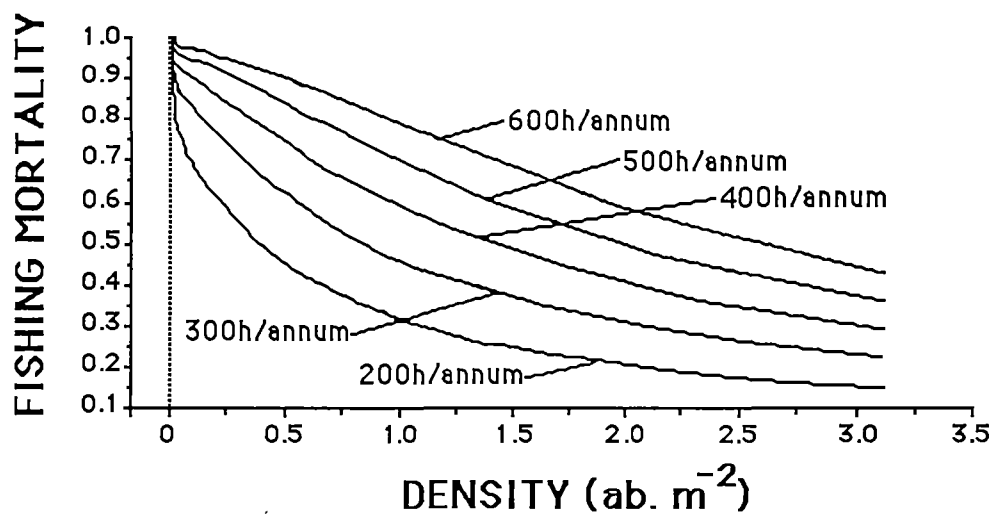


Figure 6.12
The relationship within the high productivity model between stock abundance (ab.m⁻²) and fishing mortality for varying levels of effort.

abundance declines abalone display an increasing tendency to aggregate (v. 6.2.4) and the distribution of abalone within the reef becomes increasingly heterogeneous. Because divers target these aggregations their relative efficiency increases causing fishing mortality to escalate.

This phenomenon was observed during the fish-down experiment (v. 5.3.2). The catchability of abalone in the deeper water areas was almost an order of magnitude higher than in the shallow water blocks, because the abalone in those areas were more strongly aggregated and the divers more able to target the aggregations.

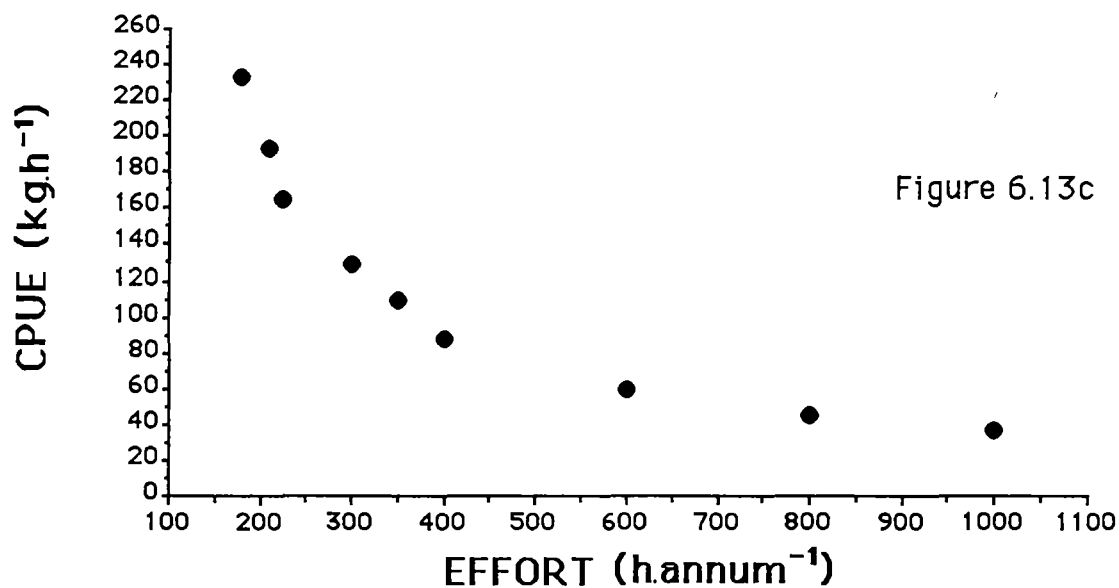
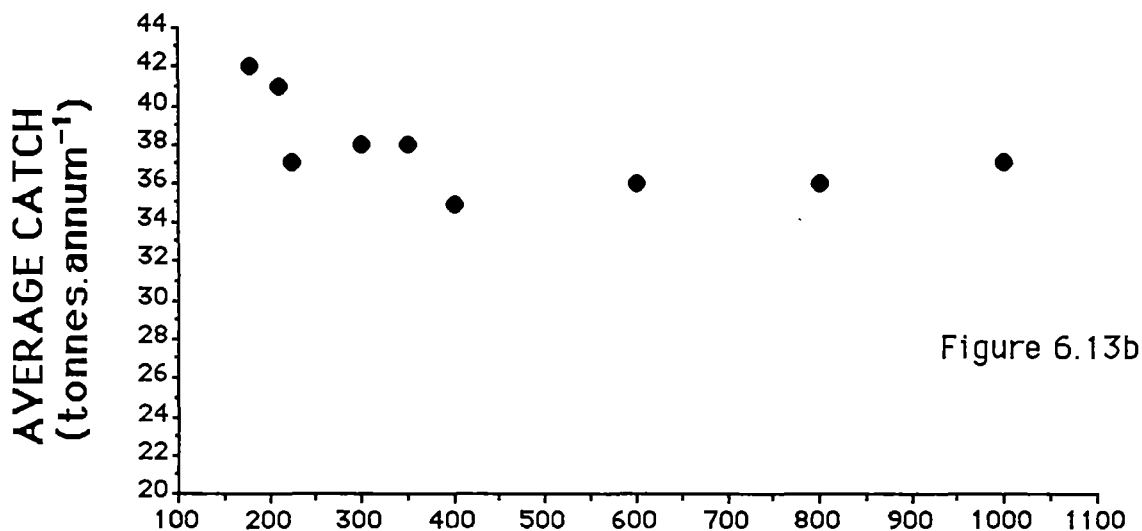
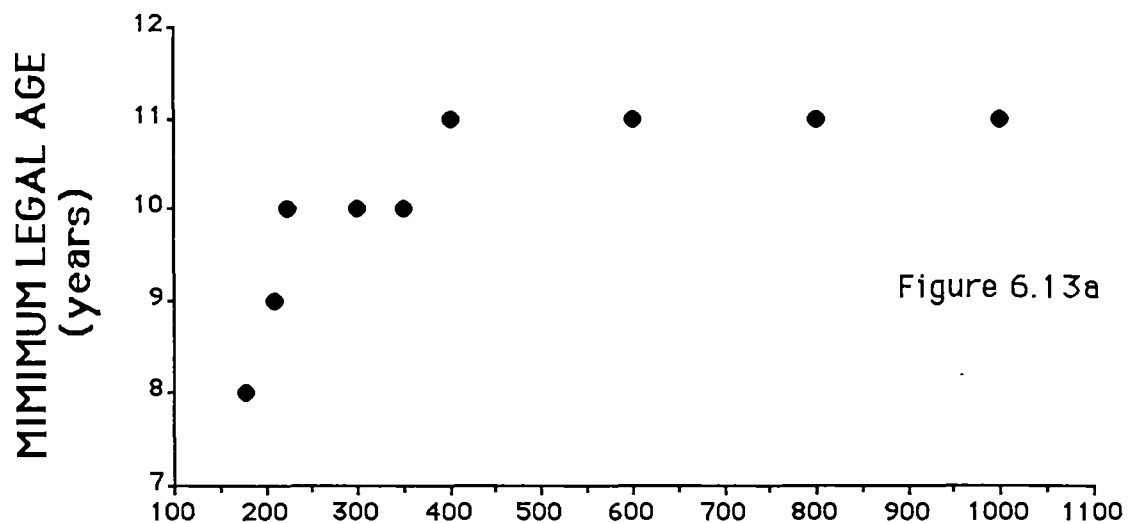
At higher levels of effort divers will tend to catch the abalone before they can re-aggregate and this effect will be less pronounced. This can be seen from Fig. 4.12 where the relationship between fishing mortality (and/or q) and stock abundance is more linear and deviates less from a constant value with higher levels of effort. Hence it is the aggregative nature of abalone leading to their heterogeneous distribution, together with the ability of divers to target aggregations which causes CPUE to be least reliable as an index of stock abundance at low exploitation rates.

6.4.4 Management Strategies

This model can also be used to examine the effectiveness of different management strategies. Historically size limits and effort restrictions have been the conservation measures most widely used in abalone fisheries and both have been employed in the Tasmanian fishery. More recently catch restrictions have been adopted. However within the context of this model, catch and effort restrictions are virtually indistinguishable and consequently I have only examined the efficacy and interrelation of size/age and effort restrictions. For this segment of the study I have used only the high productivity version of the model.

Figure 6.13 shows the characteristics, in terms of combinations of effort, minimum age, expected average catch and average CPUE for different sustainable management regimes. Figure 6.13a shows the minimum age limits necessary to sustain the varying levels of effort. From this it can be seen that size limits can be used to protect the stock from levels of effort that would otherwise not be sustained. Figure 6.13b shows the average catch expected from these sustainable combinations

Figure 6.13 Sustainable combinations of effort (h.annum^{-1}) and minimum age limit in years (a), the average annual catch (tonnes) expected from each sustainable combination (b) and the average catch rate (kg.h^{-1}) expected from each combination (c).



of effort and age limit. As expected, the harvestable yield from the stock declines slightly with increased age limits, suggesting that natural mortality is decreasing the harvestable stock at a faster rate than growth can add to it. However the decline in yield per recruit is relatively minor, approximately 10%, because of the low mortality rates of the older abalone. This robustness with regard to yield per recruit has been noted by Sluczanowski (1984) who similarly found that breeding stock levels could be greatly increased by raising size limits with a relatively small decline in yield per recruit.

The major effect of using combinations of high effort and high age limit is shown by Fig. 6.13c which depicts the average catch rate expected from the different sustainable combinations of effort and minimum age. This shows that the fishery is forced to accept extremely low catch rates if a high minimum age limit and uncontrolled effort strategies are pursued.

6.4.5 Time Delays and Management Strategies

The model also demonstrates the interaction between the type of management strategy and the timing of the strategy. Figure 6.14a shows that a complete closure of the area to fishing after 10 of 15 years of 300 h.annum^{-1} will allow recruitment to return rapidly to virgin levels. However, if the same level of fishing is allowed to continue for 20 years the recovery is greatly delayed and after 25 years of fishing is so slow as to be almost non-existent.

Likewise the affect of introducing age limit restrictions can be gauged with the model (Fig. 6.14b). A complete collapse in recruitment occurs within 20 years of commencing fishing at an effort level of 300 h.annum^{-1} and a minimum age of 8 years old. Figure 6.13a shows that a combination of a minimum age of 10 years and this level of effort would be sustainable. If the age limit is increased to 11 years after 10 years of exploitation recruitment rapidly recovers to its original level, however if 15 years of fishing are allowed before the same age limit is introduced the decline in recruitment is slowed but not reversed. To arrest the decline in recruitment at this stage without decreasing the level of exploitation an age limit of 13 years is necessary.

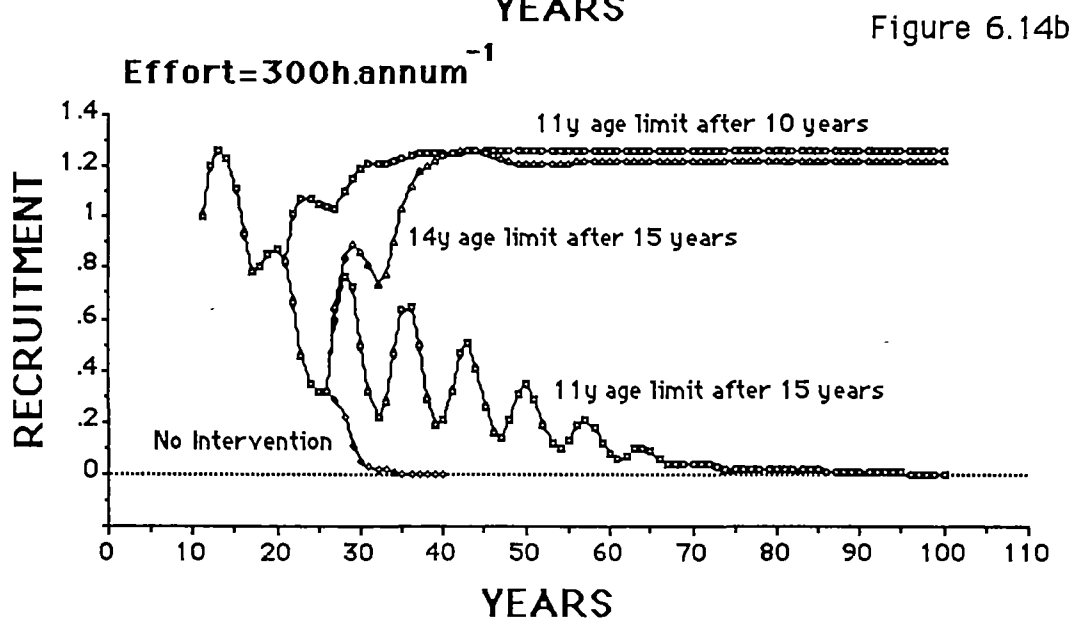
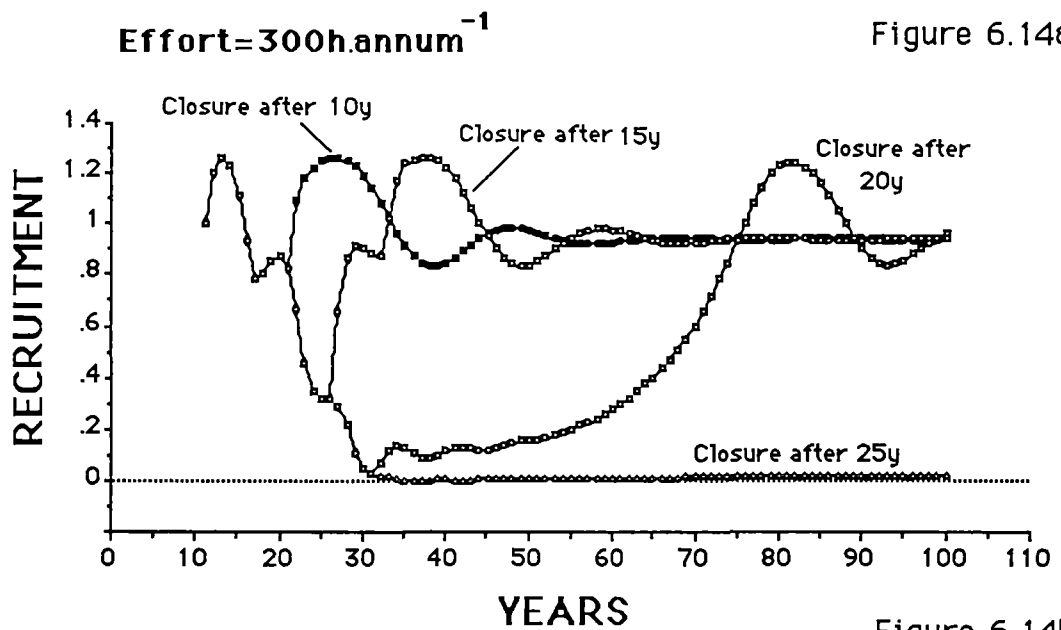


Figure 6.14

Trends in recruitment in an overexploited stock ($h.\text{annum}^{-1}=300$; legal minimum age=8), showing the effect of a complete closures after 10, 15, 20 and 25 years of fishing (a) and the effect of increasing the minimum age limit to 10 or 13 years after 10, 15, years of fishing (b).

6.5 CONCLUSIONS

Within a single population of abalone and on a temporal scale of years, interactions between their biology and the behaviour of divers are likely to cause CPUE to be a poor index of stock abundance. At high stock densities the time taken to handle abalone is liable to flatten the functional response of catch to effort. However the movement patterns of abalone and the visual nature of a diving fishery are more important, in disturbing the relationship between CPUE and stock abundance. Essentially abalone are acting as a sedentary, schooling fish. Unless fishing pressure is heavy enough to catch the abalone faster than they can aggregate, their aggregation and the ability of divers to target their aggregations will maintain CPUE at levels which do not reflect the true abundance of stock.

CHAPTER 7

THE TASMANIAN FISHERY FOR *HALIOTIS RUBRA*.

7.1 INTRODUCTION

The Tasmanian abalone fishery has been described in varying contexts and detail by Harrison (1969, 1983, 1986). In his assessment of the Tasmanian fishery for *Haliotis rubra* he concluded that the changing efficiency of the abalone divers was the most important factor affecting the relationship between catch per unit effort (CPUE) and stock abundance Harrison (1986). In an attempt to correct for this factor, he quantified these changes and standardized the measured units of effort. He used his standardized effort data, together with the surplus production analysis of Garrod (1969) and Fox (1970) to estimate the sustainable yield for the fishery. He concluded that the fishery could sustain a catch of 7 million abalone, or approximately 3 500 tonnes at the current average size.

In the previous two chapters I have presented material which suggests that a relationship does in fact exist between CPUE and stock abundance on a spatial scale of approximately 100 x 100 m and a temporal scale of days to weeks. However in the same segments, I also presented results that suggest the biology of abalone and the nature of a diving fishery severely disrupts this relationship when the spatial scale is extended to include an entire reef and/or the temporal scale is extended to years. In this chapter I describe the history and nature of the Tasmanian abalone fishery and re-examine the trends in CPUE in the light of possible factors which could have influenced these trends.

The aim of the chapter is to re-assess the importance of different factors in determining CPUE and thus address the question of to what extent CPUE can be used as an index of stock abundance in the Tasmanian abalone fishery? This fishery is particularly interesting because reliable catch and effort statistics have been kept since abalone fishing began in Tasmania in 1965. The fishery provides, therefore, an unusual opportunity to assess the value of catch and effort data in a fishery of this nature.

The uncited information presented in this chapter is of two types. The first is the catch and effort records held by the Tasmanian Department of Sea Fisheries. Fishermen are obliged by law to submit daily returns detailing the catch, number of diving hours each day and the area worked. The second is anecdotal information obtained through extensive interaction with the commercial abalone divers of Tasmania from 1983 to

1988. This information was solicited directly through formal interviews and surveys and also gained through informal discussions.

7.2 DESCRIPTION OF THE FISHERY

7.2.1 Historical Trends

Prior to 1963 the Tasmania abalone stocks were essentially unfished. Subsistence intertidal use by aboriginals had taken place for thousands of years, and during the 19th century there was minor exploitation by Chinese immigrants. In the 1950s a very small scale fishery was attempted but failed commercially. By 1963, modern diving equipment and the recognition of Asian markets provided the needed basis for the modern industry (Harrison 1983). Figure 7.1 shows the catch and effort trends in the fishery from 1965 to 1987. Total catch rose rapidly from 1963 to 1967, fluctuated between 2500 and 3500 tonnes between 1967 and 1975, and then rose steadily until 1984, when a system of individual transferable quotas was introduced to control the level of production. Effort shows essentially the same trends with somewhat less variation between 1967 and 1975.

Figure 7.2 shows the trends in catch per unit effort, measured in kg.diver-h^{-1} under water. This pattern is relatively stable, with an initial small drop in CPUE, a rise in 1970 and 1971, followed by another small decline and then minor fluctuations. If it is assumed that CPUE is proportional to abundance, the interpretation would be that there had been only a minor decline in abundance since the development of the fishery. That CPUE has remained essentially unchanged since 1974 while effort and catch have tripled, suggests either that the stock is remarkably resilient, or that CPUE is not proportional to abundance. I consider alternative interpretations of the CPUE trend in a later section, but to do this it is necessary to first examine the mechanics of the abalone fishery in more detail.

7.2.2 Modes of fishing

Some of this information has already been presented in other chapters of this thesis; however, for completeness and at the risk of some repetition, I will give a complete description of the fishery at this point.

Abalone are taken from reefs between 2 and 30 m deep around the entire coast of Tasmania. There are 125 licensed divers who must do their own diving. Divers operate

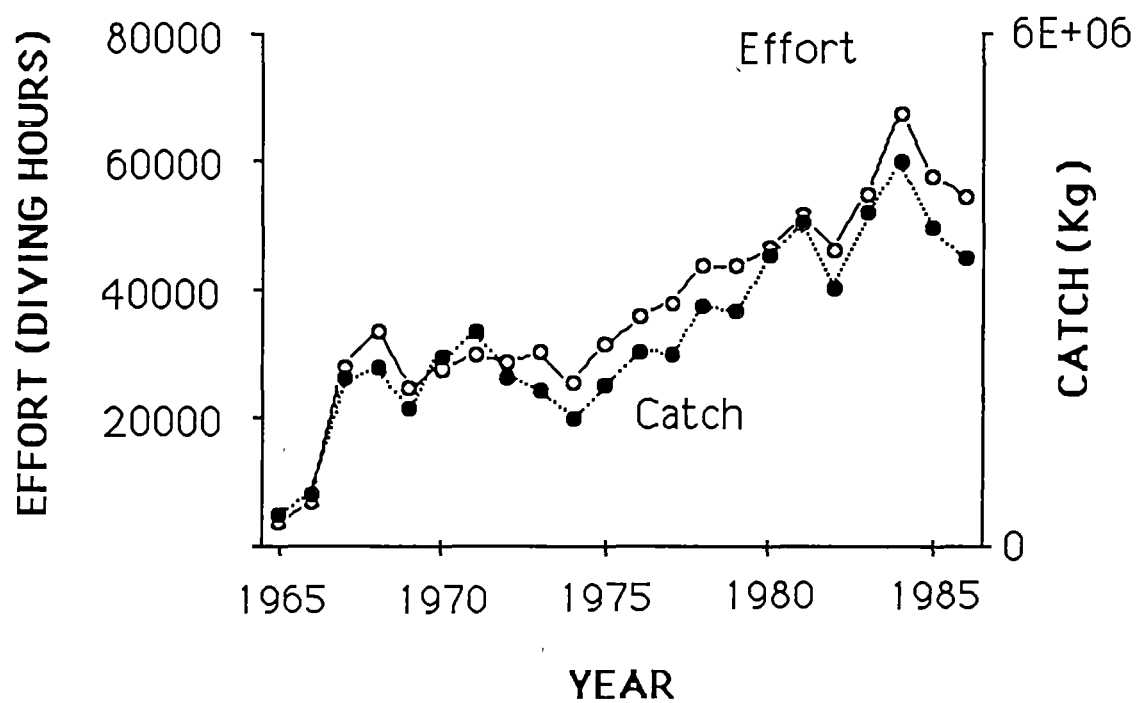


Figure 7.1
Catch (kg) and effort (h) trends in the Tasmanian abalone fishery.

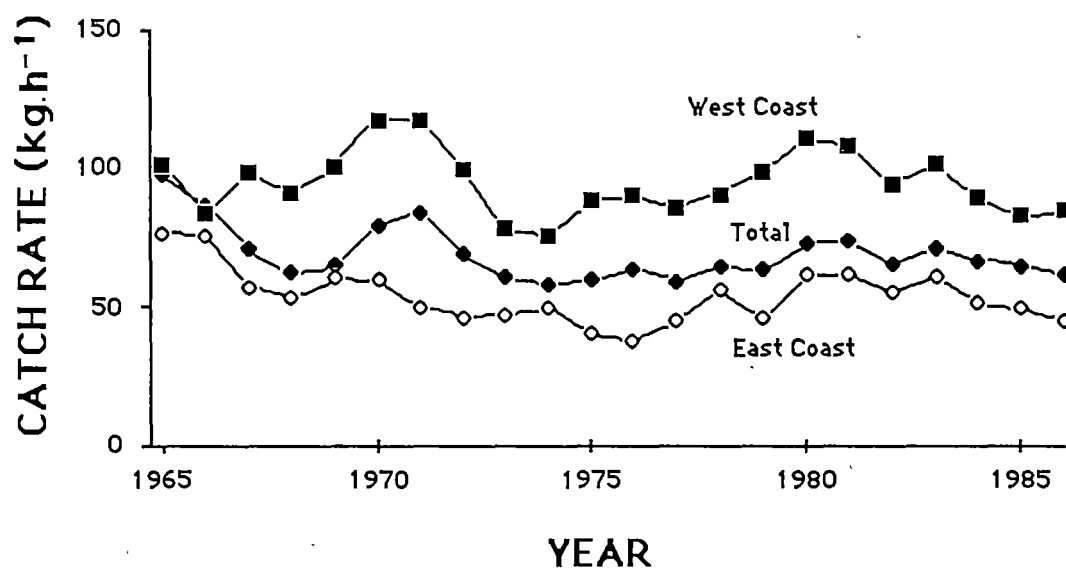


Figure 7.2
Trends in CPUE (kg.h⁻¹) in the Tasmanian abalone fishery, shown for the east and west coasts and as a state total.

from small outboard powered boats, either 4 m dinghies or 7 m runabouts, using hookah gear which pumps air to the diver from the surface. Nearly all divers employ a surface deck hand who manipulates the boat and lifts nets of harvested abalone into the vessel. The divers typically spend 4-6 h.d⁻¹ under water and move along the bottom, harvesting all abalone above the legal size limit.

Most divers prefer to undertake daily fishing trips from their home ports using the larger, twin hulled, 7 m runabouts. The range on these trips is generally up to 20-40 km from the point of launching, although distances as great as 80 km may be travelled if the weather is favourable. The best fishing grounds, however, are on the isolated west coast of Tasmania. Divers fish these areas on extended trips (3-7 days), operating from 15-30 m mother-ships, with each diver and his assistant using a 4 m dinghy for daily trips up to 15 km away from the mother-ship.

7.2.3 Spatial Structure of the Fishery

7.2.3.a Statewide Scale

Figure 7.3 shows a map of Tasmania with the statistical blocks used for the collection of abalone data. Also shown are the major home ports of abalone fishermen, with the size of the circle representing the number of divers who lived in those communities in 1986. Nearly all divers live on the east coast, which is well serviced by roads and has many small communities. In contrast, the west coast is very isolated, has only one real access point at Strahan, and is far from the major urban centres of Hobart and Launceston.

Figure 7.4 shows the distribution of abalone catch, totalled from 1965 to 1986 by statistical area. The catch comes predominantly from the west coast, with a second region of major productivity on the south and east coasts. The north coast and Flinders and King Islands are unproductive. Figure 7.5 shows the average catch rate (kg.h⁻¹) from 1965 to 1986 by statistical area. The data lump quite nicely into two groups, the west coast (blocks 5–12), and the south and east coasts (blocks 13-31). Blocks 1-4 and 32-49 can be ignored simply because the total catch in these areas is trivial. Therefore, the fishery can be considered as consisting of two major areas, the west coast which is far from home, exposed to the prevailing winds and has few safe shelters, and the east coast which is close to home, on the leeward side of Tasmania, and has many ports and protected anchorages. The west coast has high catch rates, the east coast has low catch

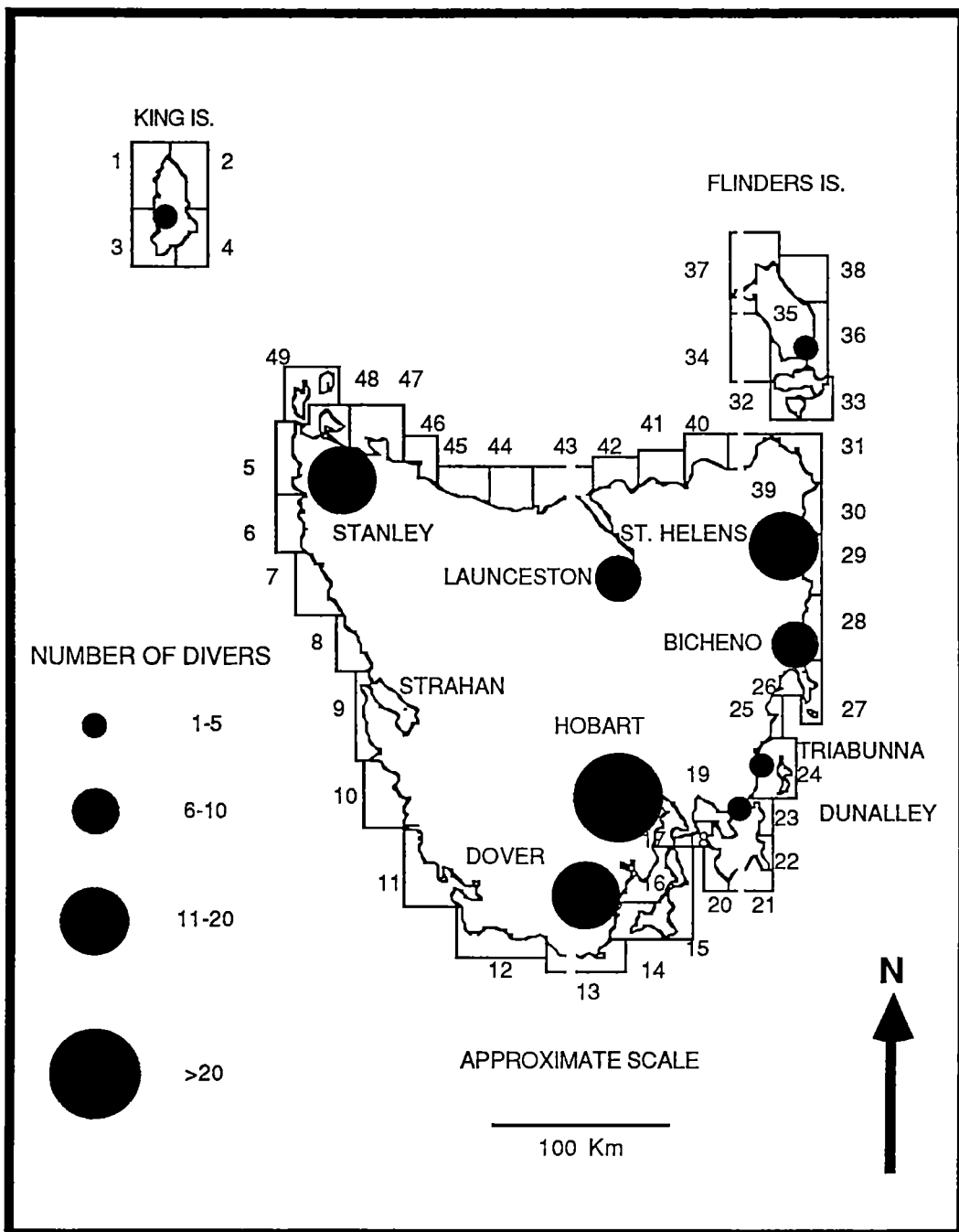


Figure 7.3
Map of Tasmania showing statistical blocks and major home ports, relative size shown for each port indicates the numbers of divers residing in each port in 1986.

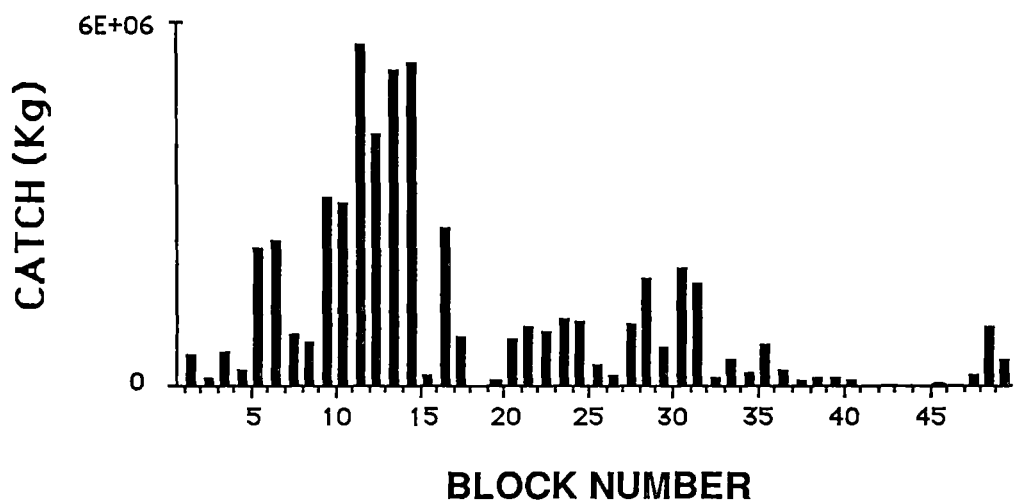


Figure 7.4
Distribution of historical catch (kg) by statistical area.

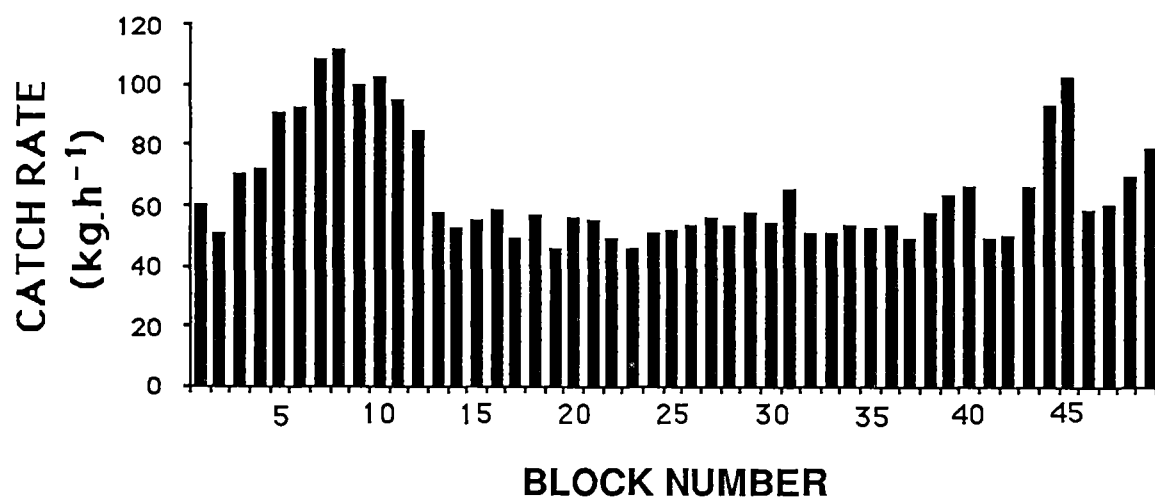


Figure 7.5
Average CPUE (kg.h⁻¹) in each statistical area.

rates.

7.2.3.b Statistical Block Scale

Spatial heterogeneity is also a feature of the fishery within the statistical blocks. Factors such as exposure to weather, distance from home or boat ramps, and catch rates are easily identifiable by the divers. Figure 7.6 shows a map of block 13, located on the southern tip of Tasmania; this statistical block includes George III Rock, the study site for Chapters 4 & 5. All vessel access in this block is from a single port with road access, and much of the block is exposed to the prevailing south-westerly wind. Interviews with fishermen in 1986/87 indicated that if they ventured west past South Cape into the most exposed region of area 13, they expected to catch approximately 80 kg.h⁻¹. Closer to port and in more protected areas they expected only 40 kg.h⁻¹. The statistical blocks therefore should not be thought of as homogeneous; the same reasons for which some statistical blocks may be preferred to others will be mirrored on a smaller scale within a statistical block.

7.2.3.c Within Reef Scale

The results of the Chapter 5 demonstrate the small scale heterogeneity which exists within abalone reefs (v. 5.3.2). These results, together with results from the study of adult movements (v. 4.3.3.c), and hypothesized larval dispersal patterns (v. 3.4.3) suggest that this heterogeneity is caused by the extremely small scale of discrete abalone populations, different habitats and variation in depths. Divers clearly recognise this heterogeneity and use it to their advantage when fishing these stocks (v. 5.3.2).

7.3 HYPOTHESES EXPLAINING CPUE TRENDS

Alternative hypotheses to explain trends in CPUE have been discussed by Harrison (1983) and include increased mechanical efficiency, motivation and skill. I begin by discussing alternative hypotheses and the details of each hypothesis. In subsequent sections I will discuss the CPUE trends in detail in an attempt to discern the relative importance of the different mechanisms.

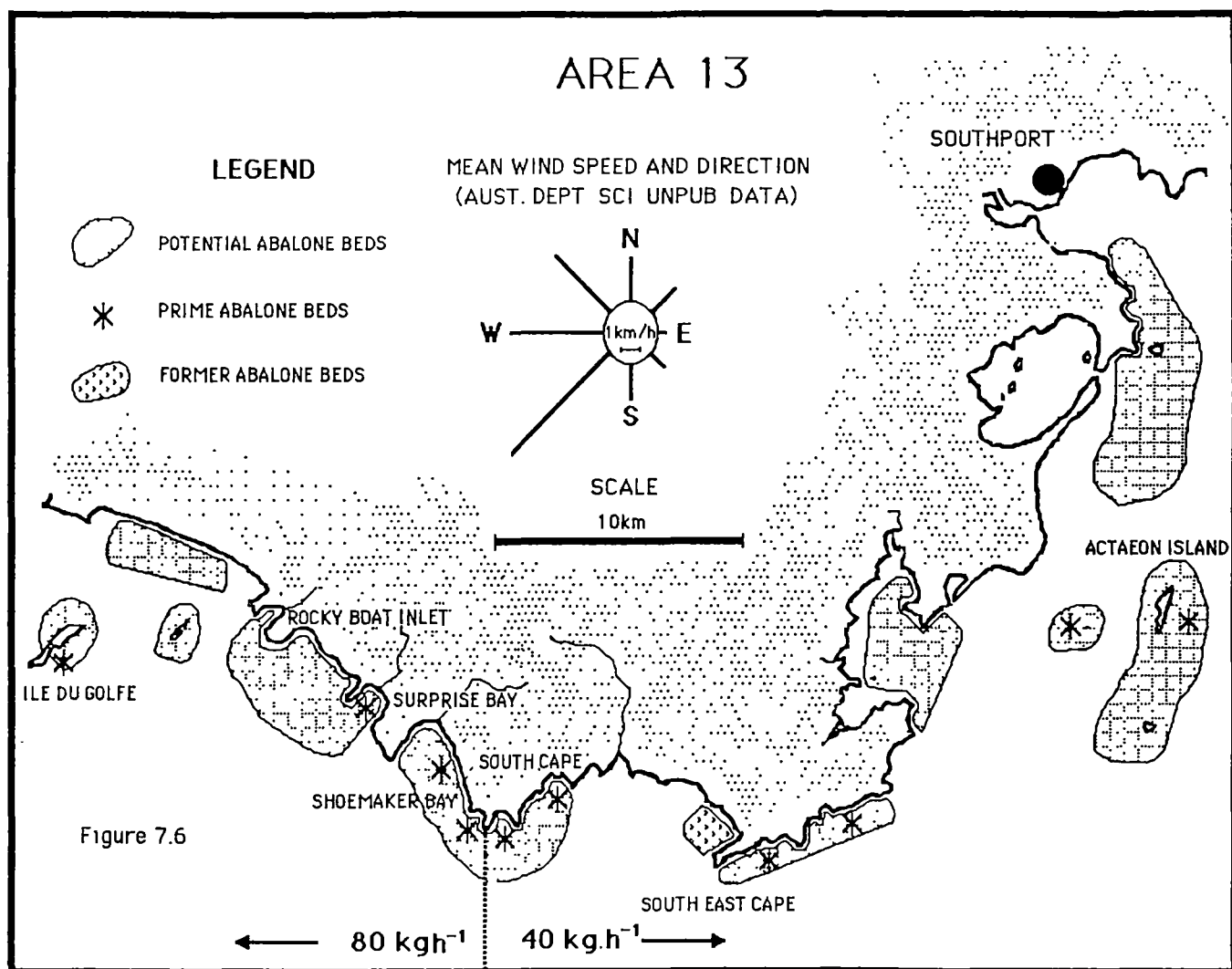


Figure 7.6
Statistical area 13 showing spatial heterogeneity of the area.

7.3.1 Increased mechanical efficiency

Two major technical changes have taken place since the beginning of the fishery: hookah equipment displaced SCUBA equipment extending the time available for diving and reducing the amount of equipment required, and divers now employ deckhands who follow them with the vessels and untangle air hoses allowing unrestricted movement. The former change took place relatively early in the history of the fishery, prior to 1969, while the latter occurred in about 1977. Another on-going change has taken place since the beginning of the fishery; diving suits have become more efficient and more comfortable, enabling divers to spend more time underwater.

These increases in mechanical efficiency can be expected to have affected the fishery in two substantially different ways. The use of hookah equipment and improvements in diving suits has increased the number of hours spent diving each day without having a major effect on the hourly catch rate. Conversely, the use of deckhands would have directly increased the catch rates without increasing the total hours worked.

7.3.2 Increasing Knowledge and Skill

Diver skill can vary within the fishery, both individually and collectively. The rudimentary skill of hookah diving is easily acquired, but the real skill of an abalone diver is his ability to quickly locate abalone stocks in unfamiliar areas and his ability to relocate these stocks in the future. In an unfamiliar environment, experienced divers are often capable of locating promising bottom types on the basis of surface topography as demonstrated during the fishing down experiment (v. 5.3.1). During a 5-10 min dive they will also be able to ascertain whether an area is worth fishing on the basis of floral characteristics and bottom topography. In contrast, a diver without these skills will have to dive randomly and may spend 60-90 min on each dive to gain the same information about abalone densities in an unfamiliar area.

Another aspect of diver skill involves the knowledge a diver accumulates about stock abundance and his general familiarity with fishing sites. This is proportional to experience and reduces the time spent searching for reefs on which to fish. Divers refer to the '70 kg barrier,' which is encountered during the first six months of their professional career. During this period, when experienced divers are catching 200-400 kg each day, a new diver will be unable to catch more than about 70 kg

because, as an unskilled diver, he must spend considerably longer searching for abalone-bearing reefs. After a few months most divers have accumulated enough knowledge to break this barrier. This phenomenon is illustrated by Fig. 7.7, which plots mean CPUE against number of months experience for 11 randomly selected divers who entered the fishery in 1984; it appears that learning is extremely rapid.

Harrison (1983), however, has suggested that diver knowledge and skill continues to increase for up to 6-7 y. This is confirmed by interviewing divers who indicated that, as their experience increased, they were not only able to memorize the location of reefs but they also pinpoint specific sites within abalone beds which they considered prime areas. In Fig. 7.6 the total area covered by abalone beds in area 13 has been indicated by cross hatching; in contrast, the stars represent the prime sites within these beds identified by a diver with 15 years experience in that area. Once an inexperienced diver has found the abalone beds, he will continue fishing the entire area until he has located and learned the position of the highest abalone concentrations within the beds. In contrast, experienced divers only fish prime sections of the abalone beds. This is in apparent contradiction to the data in Fig. 7.7, which show little change in catch rate with experience after the initial months. However, the data in Fig. 7.7 cover a relatively short time span and have no correction for the area dived. Less experienced divers may be choosing to dive in less preferable areas with higher catch rates in order to maximize their catch rates during this period, while a more experienced diver may be able to obtain similar catch rates in more preferable areas.

These skills are accumulated individually and changes in the aggregate level of individual skills can be expected to affect CPUE; but to a certain extent these skills are also accumulated by the industry collectively. For example, during the development phase of the industry, no prior knowledge existed about the location of abalone stocks and all divers were forced to find them without any direction. In the modern industry, new entrants get information from experienced divers (either by direct conversation, which can be unreliable, or by observing their diving patterns), retired divers, and experienced deckhands.

7.3.3 Diver Movement and Motivation

The spatial structure of the fishery and sedentary nature of the exploited stocks assure that movement patterns of the divers will have an important effect on catch rates.

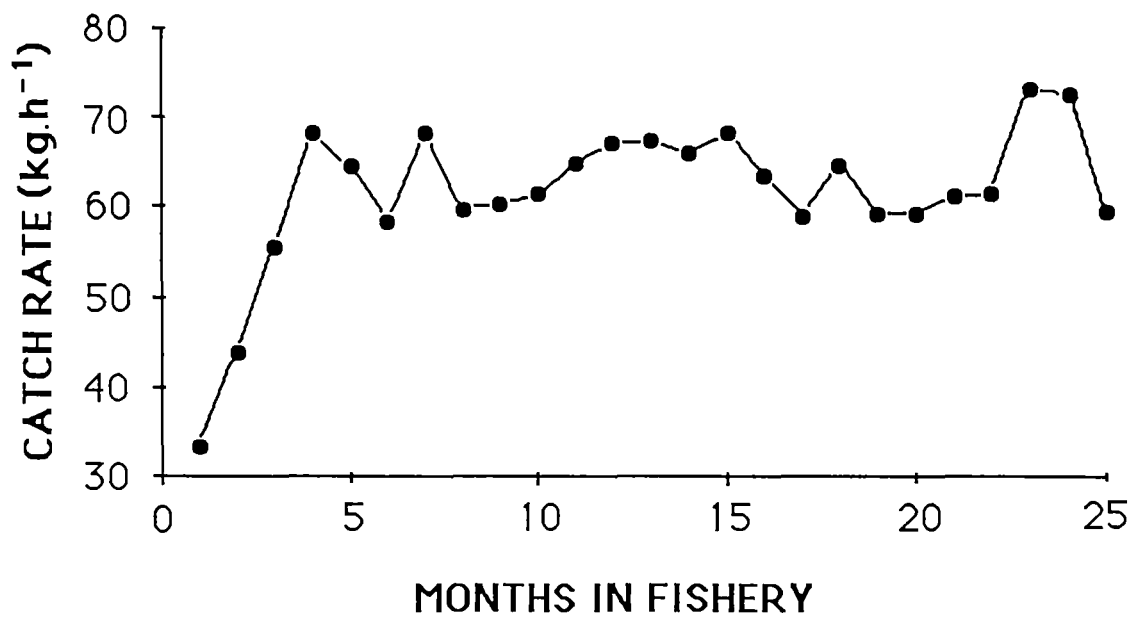


Figure 7.7
Changes in CPUE (kg.h⁻¹) with increasing diver experience.

The results of Chapter 5 demonstrated this for the small spatial scale (v. 5.3.1) and it can be expected to be a factor on a larger scale. The simplest case would be a pattern of sequential depletion, where divers simply clean out reefs that are close to harbors and anchorages and then move farther and farther away. The CPUE could easily stay constant while the total abundance declined drastically. An abalone fishery of this type would be more like mining operations than a fishery. Sequential depletion has occurred to some extent; for example, divers report that during the late 1970s to early 1980s the abalone stocks around the anchorage immediately west of South East Cape (Fig. 7.6) were fished to commercial extinction. Since that time no commercial catches have been made in that area and divers no longer attempt to fish there. However, I believe more complex interactions between movement, stock abundance and motivation of divers are continuing over the complete range of spatial scales.

Motivation is a powerful influence on the behaviour of people generally and it should be expected to influence diver behaviour as well. Collective or individual motivation will directly affect the incentive to fish for abalone. The need to earn income can be a primary influence on a diver's motivation. A diver seeks to service debts, establish himself financially, and purchase fishing equipment in the early years of his career. Later on, many of these needs may have been met and his need decreases.

The price offered for abalone has fluctuated widely at times (Fig. 7.8) and has also affected the motivation of divers. High prices encourage divers to work hard and take advantage of 'windfall profits,' while low prices may reduce or increase the motivation of divers depending on their financial need. Those with a high need may be forced to work harder, while others may choose not to land catch at the lower price.

Competition is also a source of motivation. Harrison (1983) reported that established divers without financial needs increased their fishing activity purely to compete with the new, harder working divers who entered the industry after 1974.

Motivation determines how a diver allocates his effort over a range of fishing sites. The major factors affecting this choice are listed below.

1. **Comfort and Risk:** Divers will seek to minimize their risk and maximize their comfort both within their general life style and within their diving practice. To maximize comfort, divers favour short day trips from their home ports rather than extended trips. This gives them more time to enjoy home comforts with their families. For these reasons many divers prefer to work exclusively from their home ports and avoid

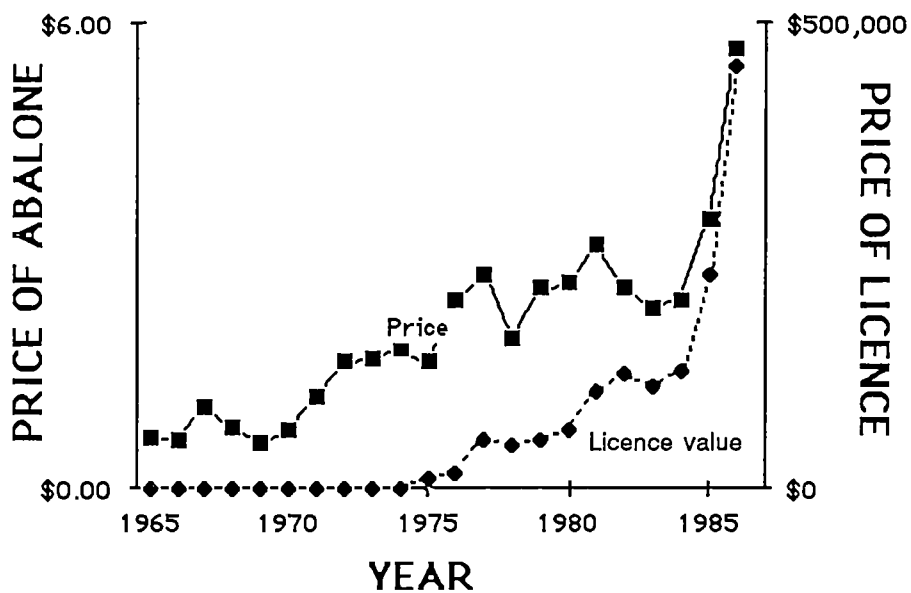


Figure 7.8
The beach price of Tasmanian abalone (\$A .kg⁻¹) and the cost of buying an entitlement to fish for abalone (\$A) in inflation adjusted (1985\$) figures.

extended trips to the west and south coasts.

Climatic conditions are important in determining comfort and risk. Adverse weather makes boat travel uncomfortable and at times dangerous and causes turbulent diving conditions. In area 13 (Fig. 7.6) divers are often not willing to or are incapable of fishing west of South Cape because of adverse winds or sea conditions. On the whole, divers say that St Helens (Fig. 7.3) is a popular home port because it is the warmest and calmest spot in the state.

A constant concern among divers are diving-related diseases, particularly dysbaric osteonecrosis, which is exacerbated by diving time and depth. This causes divers to favour diving in shallow depths (<10 meters) as already observed (v. 5.3.1).

Another concern is attack by shark, since a number of divers have been killed by white pointers (*Carcharodon carcharias*) in Tasmania. Individual divers will identify areas where they feel at risk from shark attack. The basis for labelling one area 'sharkier' than another may be personal experience, anecdotal lore, clarity of water, proximity to seal colonies, and/or open water. However, often an area will be avoided for no other reason than that it 'feels sharky' to an individual diver; this often seems to reflect a divers' unfamiliarity with an area. For all these reasons, some areas are generally recognised as 'sharky' and avoided, while others are avoided only by individual divers. In block 13 (Fig. 7.6), the area between South Cape and South East Cape is universally unpopular with divers since a fatal shark attack in 1981. Interviews with the experienced diver who provided the bulk of the information used to make Fig. 7.6 indicated that he also avoided the western side of Ile du Golfe because several divers had recently encountered a large shark in that area. This diver also avoided Rocky Boat Inlet, Surprise Bay, and Shoemaker Bay during times of freshwater runoff because then the water is murky. He also stated that for no logical reason he disliked diving on the eastern shoreline of Shoemaker Bay. It simply 'felt sharky' to him.

2. Abundance of abalone: Divers with some experience can be reasonably certain of where they will find concentrations of abalone (v. 5.3.1). Generally, within biological constraints, the greatest concentrations of abalone exist in the areas of least comfort and greatest risk because the exploitation rate is lower in those areas. In block 13 (Fig. 7.6), divers expect to catch approximately 40 kg.h⁻¹ in the eastern half of the area which is closest to the home port and the most protected from prevailing winds. However, in the western half, which is further from home port, more exposed and contains a greater

number of areas recognised as 'sharky,' the expected catch rate is 80 kg.h^{-1} .

Experienced divers allocate their effort over a continuum of areas with known comfort, risk, and stock levels. Because the stock level is inversely related to the level of comfort and proportional to risk, during times of low incentive divers will dive in safe, warm, clear, calm and shallow areas where heavy fishing pressure has reduced stock levels. Conversely, when a diver is highly motivated, he will accept greater risk and discomfort to fish areas which have not been heavily exploited. Exactly this phenomenon has already been noted in Chapter 5 (v. 5.3.1) on the scale of a single reef, with the divers involved in the fishdown experiment establishing a catch rate gradient between deep and shallow water because they prefer diving in the shallower area.

7.3.4 Functional response to abundance

Another possible reason catch rates may have stayed reasonably constant is that the functional response to abundance on a given reef may be very flat. A diver may be able to harvest roughly the same amount over a wide range of abalone abundances. The functional response of CPUE and stock abundance are plotted in Fig. 6.4; within the range of abalone densities measured during this study (c. $0.01\text{--}2.0 \text{ ab.m}^{-2}$) and on the scale of a single 'drop' or small area ($100 \times 100 \text{ m}^2$) of reef, there is a reasonably proportional relationship between CPUE and abundance (v. 6.2.5). This also conforms with the results of Chapter 5 (v. 5.3.3) where observed changes in density agreed closely with those estimated from the decline in catch rates. However, as noted by Beinssen (1979), at extremely high densities the functional response is very flat and this could have had an effect in the initial stages of the fishery.

The difficulty with this model of functional response and these parameters is that the model only describes the activities of a diver searching a given area of reef or working a single 'drop' and the catch returns gathered for the fishery do not collect data with this resolution. The catch returns require a single daily estimate of total diving hours together with a total catch. Divers vary in the way they estimate their diving hours, some using the total time away from the boat ramp, while others use total time spent in the water, still others use the total 'bottom time' (time elapsed between commencing initial descent until commencing final ascent). Each of these methods lump the multiple number of 'drops' made in any single day. For this reason it is necessary to consider the functional response on a larger temporal and spatial scale.

7.3.5 Searching Time and the Aggregation of Abalone

The results of the previous two chapters demonstrate the relatively sedentary but aggregative nature of abalone populations. The population of *H. rubra* at George III Rock displayed movement patterns (v. 4.4.5) which caused approximately 50% of the population to aggregate in 15% of the reef area (v. 5.3.2). The animals' behaviour also provides mechanisms for re-aggregation and the collapse of the area occupied by a population after fishing, together with dispersion and expansion of an unfished population (v. 4.4.5). These mechanisms, coupled with the sedentary nature of abalone populations and the high degree of knowledge that the divers have about the location of stock (v. 5.3.1) cause an increase in the catchability of abalone with decreasing density. Thus the functional response of CPUE to gross abundance levels is likely to be flattened. I have already discussed this point in Section 6.4.3. and presented simulated data derived from the population model to support this argument. These data show that CPUE will be least reliable as an index of stock abundance at lower levels of exploitation. The effect of the variability of catchability on observed CPUE is illustrated by the results of the fishdown experiment. During that experiment I observed that catch rates in deep and shallow water areas were similar despite the fact the density of abalone in the deeper areas were almost an order of magnitude lower (v. 5.3.1 & 5.3.2). This was due to the higher catchability of abalone in deeper areas where their aggregations are more marked.

7.3.6 Changing abundance

The results of Chapters 6 clearly demonstrate that at some level CPUE is determined by stock abundance (v. 6.4.3). Likewise, there can be no doubt that stock abundances have declined significantly within the Tasmanian abalone fishery. In 1988 I attended a meeting of the Tasmanian Abalone Divers Association which was called so that they could vote on a preferred level of quota for 1989. Of the 125 commercial divers in Tasmania, 72 were at the meeting. At that time I conducted a secret poll asking for their opinion as to the change of stock abundance within the period 1978-1988. On average this group of divers had 6.2 y of experience within the industry, with the range being 0-18 y. On average these divers considered that stock abundance had declined by 37% since 1978 (range 0-95%) and, if divers with less than 5 years experience were

excluded, the mean estimated decline increased to 46%.

In 1983 Harrison estimated that abundance was roughly 25% of the virgin biomass. Therefore, there can be no doubt that some of the trend in catch rates is due to changes in the level of abundance. The challenge is to sort out the relative importance of the different factors.

7.4 SPECIFIC EVENTS IN THE HISTORY OF THE TASMANIAN ABALONE FISHERY

7.4.1 Introduction

I now consider the relative importance of the different factors by examining the response of effort, catch, and CPUE in relation to a number of specific events in the fishery. In this section I have divided the history into a number of periods, characterized primarily by licensing changes and consequent changes in motivation and licence price, and discuss what I believe explains the changes that occurred during each period. This section is largely discursive, with most of the information being qualitative because of the difficulty of quantifying the factors described. However I believe the documentation of these factors, even just as plausible hypotheses, together with presentation of the circumstantial evidence for their existence can be useful for future managers of any fishery.

7.4.2 1965-1968 Development of the Fishery.

Until 1969, entry to the fishery was unlimited, an annual \$5.00 licence fee being the only requirement. There were few full-time abalone divers as most of them held full time jobs outside the fishing sector. Figure 7.2 shows the CPUE trends for the total fishery, as well as west coast and east coast areas separately. The total CPUE declined strongly during this period, dropping about 35% between 1965 and 1968. This is almost certainly due to decline in abalone abundance from the virgin state that existed at the beginning of this period. This sharp decline during the initial phase of the fishery associated with the exploitation of virgin accumulations of stock is predicted by the model I presented in Chapter 6 (v. 6.4.2). However the decline in the fishery was undoubtedly ameliorated by considerable improvement in diving equipment, practices and knowledge of the diving areas. Harrison (1983) estimated that diving efficiency was twice as high in 1969 as it had been in 1965. The flat functional response of CPUE

to 'within drop' abundance at high densities could also have been expected to attenuate this initial decline in CPUE.

Figure 7.9 shows the proportion of fishing effort on the west coast. Note that it is between 10 and 20% during this period and, while the CPUE on the west coast did not decline (see Fig. 7.2), little fishing effort was concentrated in this area during this period. These data suggest that the decline in stock abundance during this period was largely restricted to areas close to population centres since these could be fished easily during the spare time of the divers. This is consistent with what is known of the fishermen during this time; most of them were part-time divers, maintaining permanent jobs in the major population centres and diving for abalone on weekends and holidays. Consequently, it is to be expected that the majority of fishing pressure would have concentrated around the population centres of the east coast.

7.4.3 1969-1974 Limited Entry, but Non-transferable Licences

In 1969 limited entry was introduced. As a licence requirement fishermen had to earn their income primarily from the fishery, forcing them to be full-time divers. These measures, along with the introduction of an annual \$100.00 licence fee decreased the number of divers from over 250 to 120. In 1973 a further 5 restricted divers were allowed entry. The overall effort decreased between 1968 and 1969 (Fig. 7.9). The drop was not proportional to the number of divers leaving the fishery as the number of hours per diver day increased slightly (Fig. 7.10), and the number of days dived by each diver increased by approximately 40%. During this time, licences could not be transferred; a diver wishing to leave the industry relinquished his diving entitlement to the state fisheries department which re-allocated the licence to the next person on a waiting list of applicants. Because of this, very few divers left the industry during this period.

The year 1969 provides a major breakpoint in terms of professionalism and motivation. While the price of abalone remained relatively low, the divers involved had the economic need to upgrade their equipment to a professional standard and the desire to establish themselves economically. A rapid change in behaviour occurred about 1970 when effort shifted rapidly to the west coast (Fig. 7.9), site of the greatest abundance of abalone, with a resulting rise in overall CPUE. Catch rates rose significantly in 1969 and 1970 probably because of increased knowledge of the area and motivation to fish

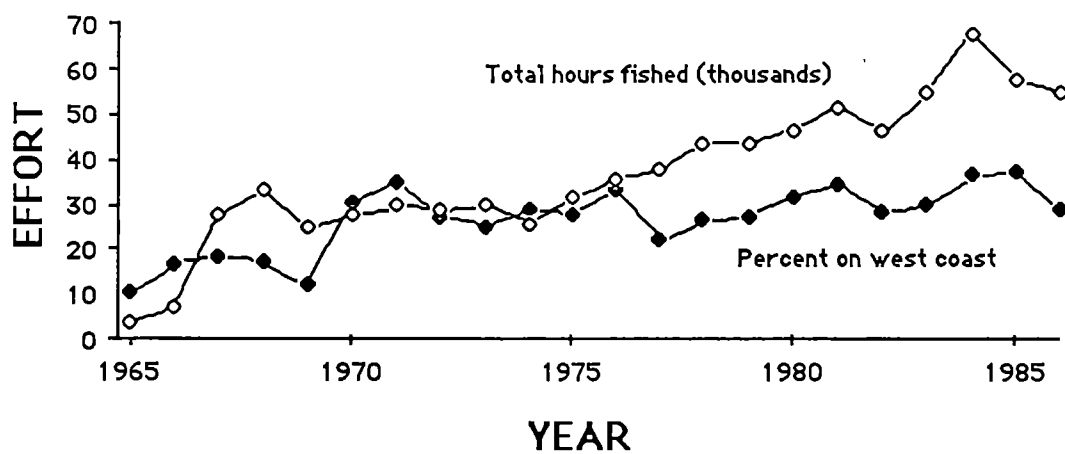


Figure 7.9

Historical trends in effort for the Tasmanian abalone fishery, showing total effort levels ($h \times 10^{-3}$) and the percent expended on the west coast for the period 1965-1985.

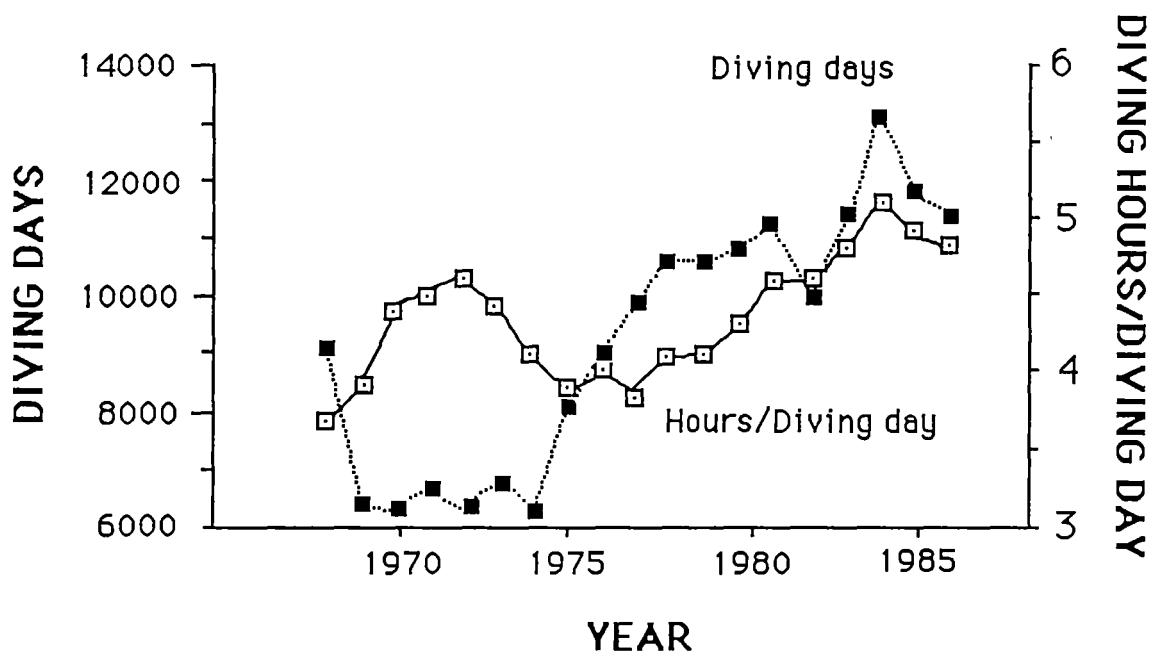


Figure 7.10
 Changes in the time (h) spent diving per diving day compared to the total number of days spent diving each year within the Tasmanian abalone fishery 1968-1985.

less desirable and less accessible areas. Even on the east coast, CPUE rose slightly in 1969 presumably for the same reasons.

Harrison (1983) also suggests that the efficiency of divers increased rapidly during this time and this is undoubtedly true. During this period divers developed modern professional diving patterns, switching from the use of SCUBA equipment to Hookah allowing longer diving hours and freed the diver from the need to change SCUBA tanks at regular intervals.

From 1972 to 1974 the CPUE declined. This may partly reflect the declining number of relatively virgin stocks remaining in the state however it is more likely to reflect the changing economic circumstances of the divers involved in the industry. The divers in the industry at this time had entered the industry at little cost and had enjoyed the benefit of virgin stocks. This helped the divers established themselves financially, pay for the equipment and plant they needed, and establish some level of economic security. Having achieved this status during the early years of limited entry, the motivation of the divers dropped considerably during 1972-1974 and they became less inclined to work under rigorous conditions. This is consistent with the fact that the number of hours dived during each diving day declined, while the number of days dived remained stable, suggesting that the divers were not prepared to get as cold each day (Fig. 7.10). Moreover, the proportion of effort expended on the weather prone and isolated west coast declined.

As the beach price for abalone rose from \$0.23.kg⁻¹ in 1969 to \$0.94.kg⁻¹ in 1974, and the divers became more aware of the health risks incurred by extensive diving, motivation continued to decline. This decline in motivation is reflected by the fact that divers began to lobby the government to allow them to nominate a person to whom their entitlement would transfer if they left the industry. In other Australian fisheries this had occurred, effectively allowing fishermen to sell their fishing entitlement on the open market. In 1972 the government announced that it would implement this system of licence transfer to promote a turnover of divers and ameliorate the effect of diving diseases, but later that year it reversed its decision. Most divers felt the change would eventually be made and those divers wishing to leave the industry remained in it anticipating a 'windfall' profit when the legislation was changed. This further decreased the divers' incentive.

Harrison (1983) explains this period of falling CPUE as a period in which

efficiency stabilized and declining stock abundance determined the trend in CPUE. However, this apparently contradicts his other statements which suggest that a diver's efficiency continues to increase for up to 8 y after they enter the industry. Most of the divers in the industry at this time had only been fishing professionally for 4-6 y at this time so that it could be expected that they would be continuing to improve their efficiency. There is also no evidence that diving equipment and technology remained static during this time; new improved equipment was becoming available to the industry all the time.

7.4.4 1975-1984 Transferable Licences

In August 1974 the government allowed divers to sell their licences to people wishing to enter the industry. This period was marked by generally rising levels of effort as divers fished more days of the year and more hours each day. This resulted in rising catches, as would be expected, but it was also associated with a slight overall rise in the CPUE, particularly on the west coast. There is evidence that a range of the factors discussed above influenced these trends.

The initial period of licence transferability was marked by an influx, particularly in 1977 (Fig. 7.11) of experienced abalone divers from the more northern Australian state of New South Wales resulting in a jump in the value of Tasmanian entitlements from \$10,000 to \$40,000. The abalone fishery in NSW was being reviewed at this time and the long-term outlook was poor, prompting many NSW divers to buy Tasmanian entitlements. These divers had a more professional approach to their diving, having come from the most competitive and heavily exploited abalone fishery in Australia. They introduced new techniques and a new competitive spirit. NSW divers expected to dive more days per year than their Tasmanian counterparts, but the ocean temperatures they were accustomed to were considerably warmer. These factors may explain why these highly motivated divers increased the total level of effort (Fig. 7.9) by increasing the total number of days worked, but not (initially) the hours dived during each day (Fig. 7.10). In 1977 the level of effort on the west coast actually declined, the only time this has occurred as general levels of effort increased. Anecdotal evidence suggests that the new divers found the abundance of abalone on the east coast high compared to NSW and initially felt little need to explore the relatively remote areas of the west coast.

Harrison (1983) suggests that the period from 1975-80 was marked by relatively rapid increase in efficiency, equivalent to a doubling in efficiency during this time. His

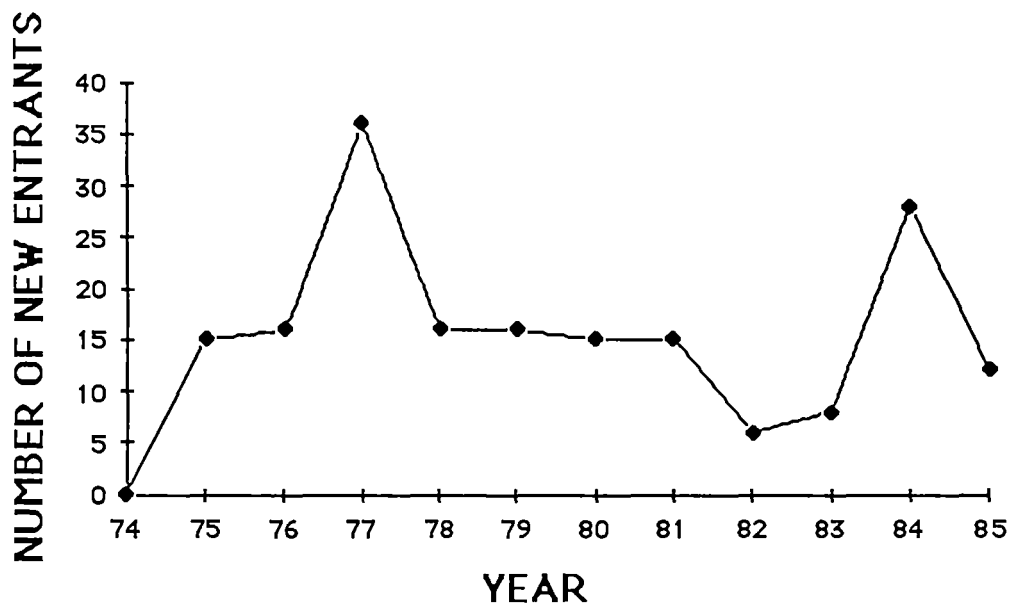


Figure 7.11
The number of new divers entering to the Tasmanian fishery for abalone between 1974 and 1985.

index of efficiency suggests that at the beginning of this period efficiency was increasing by 20% per year and that this rate slowed toward zero after 1980. However this is unlikely to be accurate; an influx of new divers between 1975-77 would have reduced the average effectiveness of divers by decreasing the level of local knowledge. The rise in CPUE observed on the east coast in 1977 undoubtedly marks the period when the major increase in efficiency occurred. Deckhands were widely adopted by the industry at this time and divers ceased to work individually from an anchored boat. After this time they worked 'live' with a deckhand following them in the boat, clearing their air hoses and lifting bags of abalone into the vessel. This new practice greatly increased the efficiency of the divers. Anecdotal evidence also suggests that in the early 1980s the illegal practice of using unlicensed divers alongside legal divers began to become more prevalent, which undoubtedly also served to bolster recorded levels of CPUE.

The new divers carried the financial burden of having to buy their way into the industry. The real (inflation adjusted) price of entitlements rose steadily during this period along with the real price of abalone, increasing the incentive and financial commitment of the divers entering the industry. Together with the increasing commitment and incentive, catches, effort and CPUE also rose during this period. The rise in the price of abalone was interrupted during 1977-78 and 1982-83 and this was mirrored by fluctuations in the price of licences. These fluctuations were also associated with variations in catch, effort, CPUE, and the hours dived in each diving day, supporting the link between financial incentive, motivation, and CPUE.

It is also evident that stock levels influenced CPUE trends in the fishery during this period. From the levels of catch and effort since 1967, the possibility that the slight rise in CPUE during this period reflected stock abundance can be discounted. However, that increasing skill, efficiency and motivation did not increase the CPUE to a greater extent obviously indicates the limitations imposed by stock abundance. This is particularly evident in the period 1983-84, when the divers were anticipating the imposition of some restrictive management policy to conserve stocks. The anticipated conservation measures had the effect of increasing divers' incentive because they tried to maximize their cash flow prior to having it restricted by legislation. Effort and catch both increased by about 20-25%, the level of effort being changed by increasing the total number of days dived and the hours dived during each day. In addition, the

percentage of effort expended on the west coast increased. These conditions were accompanied by marked and sustained increases in CPUE in 1969-70 and 1975-76, when the level of exploitation was lower, but in 1983 they resulted in only a slight increase in CPUE, and CPUE declined in 1984.

It is possible that some of this decline, or the absence of an increase in CPUE may be attributable to factors other than stock abundance. A comparison between the level of abalone reported as being exported from Tasmania, with the level of catch being reported as caught by divers, between 1974-84 indicates a discrepancy of between 8–20%, attributable to the under reporting of catch for tax purposes. This discrepancy varies over time, increasing during periods of high catch or high prices, when divers expect a greater tax burden. Divers indicate that if they under reported their catch they generally did not adjust the reported level of effort, recording the correct amount of hours dived. This would also have deflated the official estimates of CPUE during the high catches of 1982-84.

In 1984 it was announced that individual transferable quotas would be introduced in the following year. Many divers believed that the immediate reduction in the average catch from 36 tonne.diver⁻¹ to 31 tonne.diver⁻¹ would substantially reduce the value of entitlements and sold out during 1984. This led to a large number of new divers entering the industry many of whom were inexperienced as abalone divers. However it is difficult to determine what change the influx of inexperienced divers had in 1984, since it is confounded with the major structural changes caused by the introduction of ITQs.

7.4.5 1985-1986 Individual, Transferable Quotas

In 1985 a system of individual, transferable quotas (28 units.diver⁻¹ each unit being initially valued at 1.1 tonnes) was introduced. The level of catch was further reduced in 1986 (each unit being valued at 1.0 tonne). The introduction of ITQ's directly decreased the level of catch and effort and this, combined with rapidly rising prices (\$14.00.kg⁻¹ in 1986), has meant that there is less incentive for divers to dive in risky or uncomfortable areas. Divers say that the level of competition between them has gone down sharply since the introduction of ITQ's, further reducing motivation. This reduction in motivation has been associated with declining CPUE throughout the state, a fall in the percentage of fishing effort allocated to the west coast, and a reduction in

the number of hours dived each day and days dived per year. Other factors have undoubtedly also influenced the latest decline in CPUE, including the level of aggregate experience which declined through 1984, declining stock abundance and, the almost total eradication, since the introduction of ITQ's, of the use of unlicensed divers. However, since the introduction of ITQ's the under reporting of catch for tax purposes has also almost totally stopped which would tend to re-inflate estimates of CPUE.

7.5 DISCUSSION AND CONCLUSIONS

The results of Chapters 5 and 6 indicate that even on the scale of single abalone population interactions between the biology of abalone, the nature of fishermen and the natural environment could disrupt the relationship between CPUE and abundance. From the material presented in this chapter it is evident that on the larger scale of the fishery the capacity for interactions between these three facets of the fishery is even larger than suggested by these early chapters. Clearly the simple interpretation of the CPUE trend suggesting that a 30-40% decline in CPUE indicates a 30-40% decline in stock abundance from the virgin state is untenable. It is also clear that the conclusion of Harrison (1983) that, the changes in diver efficiency is the only important factor disrupting the relationship between CPUE and stock abundance has significant flaws.

The history of CPUE and effort in this fishery has been determined by complex interactions of diver behaviour, abalone biology, and changing standards of technology and knowledge. These interactions are so complex and so poorly documented that they defy quantitative analysis. For this reason the historical trends in CPUE do not seem to provide any sort of an index of stock abundance in this fishery.

However the results of Chapters 5 and 6 also indicate that some relationships do exist between catch, effort, CPUE and stock abundance on a small spatial and short temporal scale. This would seem to suggest that at some level these data can be used by managers of abalone fisheries. The results which demonstrate the level of knowledge with which divers operate raise the possibility of using patterns of effort allocation together with CPUE to provide information about stock abundance. The question which remains is whether or not the fine spatial scale required for this data to be meaningful can practically be collected from a commercial fishery?

CHAPTER 8

CONCLUSIONS

8.1 THE BIOLOGY OF *HALIOTIS RUBRA*

8.1.1 Population Structure.

The population structure of cryptic juvenile *H. rubra* which I observed during this study is not consistent with the accepted structure of abalone populations (Tegner in press.). The pre-recruit population is numerically abundant with high rates of turnover. The selection of cryptic habitats by smaller abalone observed by Witherspoon (1975) and Shepherd (1973) is apparently linked to the state of maturity of the individuals, with emergence from the cryptic habitat, onto the surface of the rocky substratum occurring at the onset of sexual maturity. It is possible that this behaviour provides a mechanism by which intra-specific interference is minimized. *H. rubra* becomes vulnerable to fishing pressure upon emergence.

I observed the onset of maturity to be age rather than size dependent, with some individuals becoming sexually mature when they are as young as 5+, however the majority were not mature until 8+ or older. Growth varied greatly between sites and even within sites could not be described with a single von Bertalanffy curve. Juvenile growth was approximately linear, or slightly sigmoidal. The growth of the mature population conformed to von Bertalanffy parameters.

The instantaneous rate of mortality for *H. rubra* apparently declines with increasing age and/or size and was found to be relatively low (0.29–0.47) for the adult population, consistent with values found in the literature.

8.1.2 Stock Dynamics and the Scale of a Unit Stock.

The level of mobility observed during this study was relatively high compared to that reported in the literature, although still low in absolute terms, with less than 30% of the abalone recaptured after 28 months at liberty, having moved more than 100 m.

Two types of movement were found. The first was a random diffusion which was apparently linked to foraging behaviour and could possibly lead to an increased tendency for abalone to disperse as food becomes limiting. The second was a directional movement with abalone showing a tendency to move towards shallower depths. This movement may cause the aggregations of *H. rubra* around shallow points of reef which are targeted by commercial divers. Together the two

documented movement patterns could provide the mechanism by which populations of *H. rubra* respond to changing population densities; aggregating to maintain sufficient densities for effective breeding and dispersing if densities exceed the resources of the habitat. Through these movement patterns it can be envisaged that abalone populations behave like a sedentary schooling fish species when exploited.

I found that approximately 70% of the observed variability in the recruitment density of 0⁺ animals could be accounted for by localized variations in the abundance of mature abalone. The most plausible explanation for this localized relationship is that larval dispersal is generally restricted. Whether or not this is true, the fact that a localized relationship exists, and the fact that adults display a limited level of mobility means that stock dynamics must be considered to occur on a spatial scale of 10's to 100's of metres.

8.2 THE FISHERY FOR *HALIOTIS RUBRA*

The results of this study demonstrate the heterogeneous distribution of *H. rubra* over the fishing ground and the level of knowledge which divers develop with experience. The divers allocate their effort with regard to this spatial heterogeneity in a highly efficient and controlled way, targeting different areas of stock according to a range of priorities, one of which is stock abundance. The manner by which divers apply effort to the stock also interacts with the stock to increase the spatial heterogeneity of the stock. Although a clear relationship exists between CPUE and stock abundance on a spatial scale of 100 x 100 m and a restricted temporal scale, the nature of the fishery introduces considerable variability to this relationship on an expanded spatial or temporal scale.

8.3 STOCK ASSESSMENT TECHNIQUES

The spatial heterogeneity of stock abundance, the behaviour of the divers and aggregative nature of abalone effectively minimize the relationship that exists between CPUE and stock abundance on the spatial and temporal scale of the catch data collected for this fishery. The history of CPUE in this fishery can be understood only if we consider motivation, spatial structure, changing abundance, changing levels of knowledge and improved technology. No one of these factors by itself is sufficient, and it is apparent that all play a role in determining CPUE trends.

I do not feel that, given the available data, it is possible to construct a useful index of abundance at this time, nor is it likely that it will ever be possible to reconstruct abundances from the historical record using trends in CPUE within this fishery.

It is possible that abalone fisheries may be one of the more difficult fisheries to analyze in the aggregate because of the nature of the resource and the fishery, however I suspect that most invertebrate and many other fisheries are similar.

To my knowledge, this is the first analysis of a fishery that considers movement patterns, spatial structure, and the motivation of the fishermen in determining CPUE. The results of this study support the argument of Hilborn (1985), that an understanding of fishermen's behaviour together with the biology of the exploited species is essential to successful fisheries management. These factors are undoubtedly relevant to many fisheries but are simply ignored .

8.4 THE DIRECTION OF FUTURE RESEARCH

If existing methods of stock assessment are not applicable for abalone stocks it is obvious that the first priority of future research must be to develop new assessment techniques.

In the short term monitoring the level of recruitment entering the fishery will indicate whether or not the fishery is stable, or declining. This would at least allow managers to pursue a trial and error form of management; reducing levels of effort while recruitment is falling and maintaining levels of effort if recruitment is stable.

In the long term I believe the fishery must be managed with an understanding of the relationship between stock and recruitment. The results of this study clearly show that if the correct spatial scale is used a relationship does exist between these two variables. If this relationship was known, the fishery could be managed to maintain levels of breeding stock which will optimize recruitment and hence production from the fishery. Periodic surveys could be used to monitor levels of breeding stock. A system of individually transferable quotas could be used to vary the size of the total catch. Zonal size limits would distribute fishing pressure within the fishery, ensuring that the correct level of fishing pressure was applied to all areas of the fishery.

However before such a management system can be implemented, considerable research is necessary. An understanding of the relationship between stock and

recruitment is essential. This will necessitate an active experimental program, which would create and maintain different levels of stock and then measure the resulting levels of recruitment. For this type of research project it is to the advantage of the biologists that the scale of a unit stock is extremely small, as this will facilitate establishing a large number of experimental populations, allowing the maximum amount of information to be gathered in the minimum period of time.

However before this sort of program, or one of monitoring recruitment levels can proceed, the whole issue of reliably measuring the abundance of this type of organism must be addressed. Obviously in order to establish and describe a relationship between levels of breeding stock and recruitment it is necessary to obtain a reliable measure of both these variables. However, in a species with an extremely heterogeneous spatial distribution obtaining reliable measurements of abundance is extremely difficult. I believe research resources should be directed towards developing and validating methods of measuring abalone abundance as the first stage of a larger program designed to describe the relationship between stock and recruitment in *H. rubra*. These methods are also necessary before a program of monitoring recruitment to the fishery commences. Without this type of basic research it is not even certain that gross changes in stock or recruitment abundance will be detected in a fashion that is statistically meaningful.

ACKNOWLEDGEMENTS

First and foremost I want to express my gratefulness to Tracy L. Sellers, Wesley B. Ford and Simon R. Talbot for their enthusiastic support of me during this study. This study is primarily based on their labour; they took the brunt of what, at times, seemed like endless days beneath the cold water.

Acknowledgements are also due to the Tasmanian Department of Sea Fisheries and the Fishing Industry Research Trust Account for providing me with the resources needed to complete this study.

I also need to acknowledge the role of my supervisor Dr R.W.G. White. Thanks also go to Mr J.C. Sanderson for assistance with all things botanical, and Mr G. Hyndes for his assistance with the feeding studies.

I wish particularly to thank the abalone divers of Australia and New Zealand generally but particularly, Tasmania, for talking to me and continuing to tell me all their best ideas, even though I took so long to grasp the concepts. I also need to acknowledge the role of the Tasmanian Abalone Divers' Research and Development Trust in supporting me financially.

Thanks also go out to a large body of other friends and acquaintances who variously:

- provided labour in one form or another,
- allowed me to bounce ideas off them,
- gave me ideas,
- tried to make me see sense and
- taught me the skills and concepts I needed to know.

In this context I should particularly thank Professors Carl J. Walters and Ray Hilborn for their teaching and for so generously allowing me to steal most of 'my' best ideas from them.

Finally thanks to Helen who allowed herself to be dragged to Tasmania, so I could undertake this study; and then completed a law degree to fill in time. Thanks go to her for her proof-reading skills and for being there most of the time.

REFERENCES

- Anderson, E.K. & North, W.J. (1966). *In situ* studies of spore production and dispersal in the giant kelp, *Macrocystis*. *Proc. Int. Seaweed Symp.* **5**, 73–86.
- Ault, J.S. & Demartini, J.D. (1987). Movement and dispersion of red abalone *Haliotis rufescens*, in northern California. *Calif. Fish Game* **73**, 196–213.
- Beinssen, K. (1979). Fishing power of divers in the abalone fishery of Victoria, Australia. *Rapp. P.-v. Reun. Cons. int. Explor. Mer* **175**, 20–22.
- Beinssen, K. & Powell, D. (1979). Measurement of natural mortality in a population of blacklip abalone, *Notohaliotis ruber*. *Rapp. P.-v. Réunion. Cons. perm. int. Explor. Mer* **175**, 23–26.
- Berg, J. (1979). Discussion of methods of investigating the food of fishes with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). *Mar. Biol.* **50**, 263–273.
- Berg, C.J. & Alatalo, P. (1985). Biology of the tropical bivalve *Asaphis deflorata* (Linne, 1758). *Bull. mar. Sci.* **37**, 827–838.
- Beverton, R. J. H., & Holt, S. J. (1957). On the dynamics of exploited fish populations. *U.K. Min. Agr. Fish., Fish. Invest. (Ser. 2)* **19**, 1–533.
- Breen, P. A. (1986). Management of the British Columbia fishery for northern abalone (*Haliotis kamschatkana*). *Can. Spec. Publ. Fish. Aquat. Sci.* **92**, 300–312.
- Breen, P. A. & Adkins, B. E. (1980). Spawning in a British Columbia population of northern abalone, *Haliotis kamschatkana*. *Veliger* **23**, 177–179.
- Braaten, D.O. (1969). Robustness of the Delury population estimator. *J. Fish. Res. Bd Can.* **26**, 339–352.
- Chapman, D.G., Fink, B.D. & Bennett, E.B. (1965). A method for estimating the rate of shedding of tags from yellowfin tuna. *Inter-Amer. Trop. Tuna Comm. Bull.* **10**, 335–352.
- Clavier, J. & Richard, O. (1984). Etude expérimentale du déplacement de l'ormeau (*Haliotis tuberculata*) dans la milieu naturel. *Rev. Trav. Inst. Pêches marit.* **46**, 315–26.
- Clavier, J. & Richard, O. (1986a). Estimation du stock naturel d'ormeaux (*Haliotis tuberculata*) dans la région de Saint-Malo. *Rev. Trav. Inst. Pêches marit.* **48**, 95–105.

- Clavier, J. & Richard, O. (1986b). Growth of juvenile *Haliotis tuberculata* (Mollusca: Gastropoda) in their natural environment. *J. mar. biol. Ass. U.K.* **66**, 497-503.
- Connell, J.H. (1985). The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J. exp. mar. Biol. Ecol.* **93**, 11-45.
- Cox, K.W. (1962). California abalones, Family Haliotidae. *Fish. Bull. Calif. Dep. Fish & Game* No. **118**, 1-131.
- Creese, R.G. (1981). Patterns of growth, longevity and recruitment of intertidal limpets in New South Wales. *J. exp. mar. Biol. Ecol.* **51**, 145-171.
- Creese, R.G. & Ballantine, W.J. (1983). An assessment of breeding in the intertidal limpet, *Cellana radians* (Gmelin). *J. exp. mar. biol. Ecol.* **67**, 43-59.
- Day, R.W. & Quinn, G.P. (in prep.). Comparison of means after an ANOVA. *Ecol. Monogr.*
- Dayton, P.K. (1973). Dispersion, dispersal, and persistence of the annual intertidal alga, *Postelsia palmaeformis* Ruprecht. *Ecology* **54**, 433-438.
- Dayton, P.K., Currie, V., Gerrodette, T., Keller, B.D., Rosenthal, R. & Ven Tresca, D. (1984). Patch dynamics and stability of some California kelp communities. *Ecol. Monogr.* **54**, 253-289.
- Deevey, E.S. (1947). Life tables for natural populations of animals. *Q. Rev. Biol.* **22**, 283-314.
- DeLury, D.B. (1947). On the estimation of biological populations. *Biometrics* **3**, 145-167.
- Doi, T.S., Guzmán del Prío, S.A., Marín, V., Ortíz, M.Q., Camacho, J.A. & Muñoz, y T.L. (1977). Analisis de la poblacion y diagnostico de la pesqueria de abulon amarillo (*Haliotis corrugata*) en el area de Punta Abreojos e Isla Cedros, B.C. *Serie cient. Dir. gen. Inst. nac. Pesca, Mex.* No. **18**
- Draper, N. & Smith, H. (1966). Applied regression analysis. Wiley Interscience. New York.
- Ebert, E.E., & Houk, J.L. (1984). Elements and innovations in the cultivation of red abalone *Haliotis rufescens*. *Aquaculture* **39**, 375-392.
- Fabens, A.J. (1965). Properties and fitting of the von Bertalanffy growth curve. *Growth* **29**, 265-289.
- FAO (1963). Yearbook of fisheries statistics. Catch & landings. UNFAO. No. **16**, C63

- FAO (1973). Yearbook of fisheries statistics. Catch & landings. UNFAO. No. **35**, 485–487.
- FAO (1976). Yearbook of fisheries statistics. Catch & landings. UNFAO. No. **42**, 127.
- FAO (1980). Yearbook of fisheries statistics. Catch & landings. UNFAO. No. **52**, 193.
- FAO (1984). Yearbook of fisheries statistics. Catch & landings. UNFAO. No. **56**, 243–244.
- Fedorenko, A.Y., & Sprout, P.E. (1982). Abalone biology, fishery regulations, commercial catch (1952-1980), and current state of resource in British Columbia. *Can. Man. Rep. Fish. Aquat. Sci.* No. **1658**, 1-73.
- Forster, G.R. (1967). The growth of *Haliotis tuberculata*: results of tagging experiment in Guernsey 1963-65. *J. mar. biol. Ass. U.K.* **47**, 287-300.
- Forster, G.R., Potts, G.W. & Swinfen, R. (1982). Changes in the ormer populations of Guernsey and Jersey. *J. Mar. Biol. Ass. U.K.* **62**, 717-27.
- Fournier, D.A. & Breen, P.A. (1983). Estimation of abalone mortality rates with growth analysis. *Trans. Am. Fish. Soc.* **112**, 403-411.
- Fox, W.W. (1970). An exponential surplus yield model for optimizing exploited fish populations. *Trans. Am. Fish. Soc.* **99**, 80-88.
- Francis, R.I.C.C. (1988). Are growth parameters estimated from tagging and age length data comparable? *Can. J. Fish. Aquat. Sci.* **45**, 936-42.
- Fujino, K. (1978). Genetics studies on the Pacific Abalone. I. Inbreeding and overdominance as evidenced by biochemical polymorphism in a wild population. *Bull. Jap. Soc. Sci. Fish.* **44**, 357-361.
- Fujio, Y., Yamanaka, R., & Smith, P.J. (1983). Genetic variation in marine molluscs. *Bull. Jap. Soc. Sci. Fish.* **49**, 1809-1817.
- Garland, C.D., Cooke, S.L., Grant, J.F. & McMeekin, T.A. (1985). Ingestion of the bacteria on the cuticle of crustose (non-articulated) coralline algae by post-larval and juvenile abalone (*Haliotis ruber* Leach) from Tasmanian waters. *J. exp. mar. Biol. Ecol.* **91**, 137-149.
- Garrod, D.J. (1969). Empirical assessments of catch/effort relationships in North Atlantic cod stocks. *Res. Bull. Int. Comm. Northw. Atlant. Fish.* **6**, 26–34.
- Gerrodette, T. (1981). Dispersal of the solitary coral *Balanophyllia elegans* by demersal planular larvae. *Ecology* **62**, 611-619.
- Grant, J.F. (1981). Abalone culture in Japan: Development and current commercial

- practise. *Tas. Fish. Res.* **23**, 1-17.
- Gulland, J.A. (1969). Manual of methods for fish stock assessment. Part 1. Fish population analysis. *F.A.O. Man. Fish. Sci.* No. **4**. 1-154.
- Gulland, J.A. (1977). The analysis of data and development of models. in '*Fish Population Dynamics*'. (ed. J.A. Gulland.) pp 67-95. (Wiley: New York.).
- Hancock, D.A. (1979). Population dynamics and management of shellfish stocks. *Rapp. P. -v. Reun. Cons. Int. Explor. Mer* **175**, 8-19.
- Harrigan, J.F. (1972). Behaviour of the planula larva of the scleractinian coral *Pocillopora damicornis* (L.). *Am. Zool.* **12**, 723.
- Harrison, A.J. (1969). Australian abalone industry. *Aust. Fish. Reprint* 1969.
- Harrison, A.J. (1983). The Tasmanian abalone fishery. *Tas. Fish. Res.* No. **26**.
- Harrison, A.J. (1986). Gastropod fisheries of the Pacific with particular reference to Australian abalone. *Can. Spec. Publ. Fish. Aquat. Sci.* **92**, 14-22.
- Harrison, A.J. & Grant, J.F. (1971). Progress in abalone research. *Tas. Fish. Res.* **5**, 1-10.
- Hayashi, I. (1980a). Structure and growth of a shore population of the ormer, *Haliotis tuberculata*. *J. mar. biol. Ass. U.K.* **60**, 431-437.
- Hayashi, I. (1980b). The reproductive biology of the ormer, *Haliotis tuberculata*. *J. mar. biol. Ass. U.K.* **60**, 415-430.
- Hilborn, R. (1985). Fleet dynamics and individual variation: why some people catch more fish than others. *Can. J. Fish. Aquat. Sci.* **42**, 2-13.
- Hilborn, R., & Walters, C.J. (1987). A general model for simulation of stock and fleet dynamics in spatially heterogenous fisheries. *Can. J. Fish. Aquat. Sci.* **44**, 1366-1369.
- Hines, A.H. & Pearse, J.S. (1982). Abalones, shells, and sea otters: dynamics of prey populations in central California. *Ecology* **63**, 1547-1560.
- Ino, T. (1952). Biological studies on the propagation of the Japanese abalone (genus *Haliotis*). *Bull. Tokai Reg. Fish. Res. Lab.* **5**, 29-102.
- Jackson, G.A., & Strathmann, R.R. (1981). Larval mortality from offshore mixing as a link between precompetent and competent periods of development. *Am. Nat.* **118**, 16-26.
- Jensen, J.T. (1981). Distribution, activity, and food habits of juvenile *Tegula funebris* and *Littorana scutulata* (Gastropoda: Prosobranchia) as they relate to

- resource partitioning. *Veliger* **23**, 333-338.
- Keough, M.J. & Downes, B.J. (1982). Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia* **54**, 348-352.
- Knight-Jones, E.W. (1953). Decreased discrimination during setting after prolonged planktonic life in larvae of *Spirorbis borealis* (Serpulidae). *J. mar. biol. Ass. U.K.* **32**, 337-345.
- Knowlton, N., & Keller, B.D. (1986). Larvae which fall short of their potential: highly localized recruitment in an alpheid shrimp with extended larval development. *Bull. Mar. Sci.* **39**, 213-223.
- Koike, Y. (1978). Biological and ecological studies on the propagation of the ormer, *Haliotis tuberculata* Linnaeus 1. Larval development and growth of juveniles. *La Mer (Tokyo)* **16**, 124-36.
- Leighton, D.L. & Boolootian, R.A. (1963). Diet and growth in the black abalone, *Haliotis cracherodii*. *Ecology* **44**, 227-238.
- Leighton, D.L. (1972). Laboratory observations on the early growth of the abalone, *Haliotis sorenseni*, and the effect of temperature on larval development and settling success. *Fish. Bull.* **70**, 373-381.
- Leighton, D.L. (1974). The influence of temperature on larval and juvenile growth in three species of southern California abalones. *Fish. Bull.* **72**, 1137-1145.
- Leslie, P.H. & Davis, D.H.S. (1939). An attempt to determine the absolute number of rats on a given area. *J. Animal Ecol.* **8**, 94-113.
- Macdonald, P.D.M., & Green, P.E.J. (1985). *Mix 2.2: An Interactive Program for Fitting Mixtures of Distributions*. Ichthus Data Systems, Hamilton, Ontario.
- Macdonald, P.D.M. & Pitcher, T.J. (1979). Age-groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. *J. Fish. Res. Bd Can.* **36**, 987-1001.
- Matthews, J.H. & Volframs, A. (1978). Investigating the physical aspect of bays and estuaries: a study of the hydrology and hydrodynamics of North West Bay. *Univ. Tas. Env. Stud. Occ. Pap.* No. **7**, 1-53.
- McShane, P.E., Beinssen, K.H.H., Smith, M.G., O'Connor, S. & Hickman, N.J. (1986). Reproductive biology of blacklip abalone *Haliotis ruber* Leach from four Victorian populations. *Mar. Sci. Lab. Tech. Rep.* No. **55**. 1-13.
- McShane, P.E., Black, K.P. & Smith, M.G. (1988). Recruitment processes in *Haliotis rubra* (Mollusca : Gastropoda) and regional hydrodynamics in southeastern

- Australia imply localized dispersal of larvae. *J. exp. mar. Biol. Ecol.* **124**, 175-203.
- Menge, B.A. (1975). Brood or broadcast? The adaptive significance of different reproductive strategies in the two intertidal sea stars *Leptasterias hexactis* and *Pisaster ochraceus*. *Mar. Biol.* **31**, 87-100.
- Mileikovsky, S.A. (1971). Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Mar. Biol.* **10**, 193-213.
- Millar, R.H. & Hollis, P.J. (1963). Abbreviated pelagic life of Chilean and New Zealand oysters. *Nature* **197**, 512-513.
- Momma, H. & Sato, R. (1969). The locomotion behaviour of the disc abalone, *Haliotis discus hannai* Ino, and the Siebold's abalone, *Haliotis sieboldi* Reeve, in the fishing grounds. *Tohoku J. Agric. Res.* **20**, 150-157.
- Moore, P.G. (1975). The role of habitat selection in determining the local distribution of animals in the sea. *Mar. Behav. Physiol.* **3**, 97-100.
- Mottett, M.G. (1978). A review of the fishery biology of abalones. *Wash. Dept. Fish. Tech. Rep. No. 37*. 1-81.
- Newman, G.G. (1966). Movements of the South African abalone. *Invest. Rep. Div. Sea Fish. S. Afr. No. 56*. 1-20.
- Newman, G.G. (1967). Reproduction of the South African abalone *Haliotis midae*. *Invest. Rep. Div. Sea Fish. S. Afr. No. 64*. 1-24.
- Newman, G.G. (1968). Growth of the South African abalone *Haliotis midae*. *Invest. Rep. Div. Sea Fish. S. Afr. No. 67*. 1-24.
- Olson, R.R. (1985). The consequences of short-distance larval dispersal in a sessile marine invertebrate. *Ecology* **66**, 30-39.
- Osborne, M.R. (1976). Nonlinear least squares - the Levenberg algorithm revisited. *J. Aust. Math. Soc. Ser. B.* **19**, 343-357.
- Palmer, A.R. & Strathmann, R.R. (1981). Scale of dispersal in varying environments and its implications for life histories of marine invertebrates. *Oecologia* **48**, 308-318.
- Paloheimo, J.E. & Dickie, L.M. (1964). Abundance and fishery success. *Rapp. P.-v. Reun. Cons. Int. Explor. Mer* **155**, 152-163.
- Pearse, J.S. (1969). Slow developing demersal embryos and larvae of the antarctic sea

- star *Odontaster validus*. *Mar. Biol.* **3**, 110-116.
- Peck, L.S., Culley, M.B., Helm, M.M. (1987). A laboratory energy budget for the former *Haliotis tuberculata* L. *J. exp. mar. Biol. Ecol.* **106**, 103-124.
- Poore, G.C.B. (1972a). Ecology of New Zealand abalones, *Haliotis* species (Mollusca: Gastropoda). 2. Seasonal and diurnal movement. *N.Z. J. mar. Freshwater Res.* **6**, 246-258.
- Poore, G.C.B. (1972b). Ecology of New Zealand abalones *Haliotis* species (Mollusca : Gastropoda). 3. Growth. *N.Z. J. mar. Freshwater Res.* **6**, 534-559.
- Poore, G.C.B. (1972c). Ecology of New Zealand abalones *Haliotis* species (Mollusca : Gastropoda). 1. Feeding. *N.Z. J. mar. Freshwater Res.* **6**, 11-22.
- Poore, G.C.B. (1973). Ecology of New Zealand abalones, *Haliotis* species (Mollusca: Gastropoda). 4. Reproduction. *N.Z. J. mar. Freshwater Res.* **7**, 67-84.
- Powell, E.N., Cummins, H., Stanton, R.J. & Staff, G. (1984). Estimation of the size of molluscan settlement using the death assemblage. *Est. Coast. Shelf Sci.* **18**, 367-384.
- Prager, M.H., Saila, S.B. & Recksiek, C.W. (1987). FISHPARM: a microcomputer program for parameter estimation of nonlinear models in fishery science. *Old Dominion Univ. Res. Found. Tech. Rep.* No. **87-10**, 1-37.
- Prince, J.D. & Ford, W.B. (1985). Use of anaesthetic to standardize efficiency in sampling abalone populations (genus *Haliotis*; Mollusca : Gastropoda). *Aust. J. mar. Freshwater Res.* **36**, 701-706.
- Prince, J.D., Sellers, T.L., Ford, W.B. & Talbot, S.R. (1988). A method for ageing the abalone *Haliotis rubra* (Mollusca : Gastropoda). *Aust. J. mar. Freshwater Res.* **39**, 167-175.
- Quayle, D.B. (1971). Growth, morphometry and breeding in the British Columbia abalone (*Haliotis kamtschatkana* Jonas). *Tech. Rep. Can. Fish. Res. Bd.* No. **279**. 1-84.
- Ricker, W.E. (1954). Stock and recruitment. *J. Fish. Res. Bd Can.* **11**, 559-623.
- Ricker, W.E. (1977). The Historical Development. In '*Fish Population Dynamics*'. (ed. J.A. Gulland.) pp.1-12. (Wiley: New York.).
- Ricker, W.E. (1979). Growth rates and models. in '*Fish Physiology*' Vol. 8 pp. 678-738. Hoar, Randall and Brett (eds.). (Academic Press: New York) .
- Rothschild, B.J. (1977). Fishing effort. In '*Fish Population Dynamics*'. (ed. J.A.

- Gulland.) pp. 96-115. (Wiley: New York.).
- Russell, E.S. (1931). Some theoretical considerations on the 'overfishing' problem. *J. Cons. Int. Explor. Mer* **6**, 3-20.
- Sainsbury, K.J. (1982a). Population dynamics and fishery management of the paua, *Haliotis iris* I. Population structure, growth, reproduction, and mortality. *N.Z. J. mar. Freshwater Res.* **16**, 147-161.
- Sainsbury, K.J. (1982b). Population dynamics and fishery management of the paua, *Haliotis iris* II. Dynamics and management as examined using a size class population model. *N.Z. J. mar. Freshwater Res.* **16**, 163-173.
- Saito, K. (1981). The appearance and growth of 0-year-old Ezo abalone. *Bull. Jap. Soc. Sci. Fish.* **47**, 1393-1400.
- Sanders, M.J. & Morgan, A.J. (1976). Fishing power, fishing effort, density, fishing intensity and fishing mortality. *J. Cons. int. Explor. Mer* **37**, 36-40.
- Sanderson, C.J. & Thomas, D.P. (1987). Macroalgal communities in the D'entrecasteaux Channel, Tasmania. *Aust. J. Ecol.* **12**, 41-51.
- Sarver, D.J. (1979). Recruitment and juvenile survival in the sea hare *Aplysia juliana* (Gastropoda: Opisthobranchia). *Mar. Biol.* **54**, 353-361.
- Seager, J.R. (1982). Population dynamics of the antarctic opisthobranch *Philine gibba* Strebel. *J. exp. mar. Biol. Ecol.* **60**, 163-179.
- Sebens, K.P. (1983). The larval and juvenile ecology of the temperate octocoral *Alcyonium siderium* Verrill. I. Substratum selection by benthic larvae. *J. exp. mar. Biol. Ecol.* **71**, 73-89.
- Seki, T. & Kan-no, H. (1981a). Induced settlement of the Japanese abalone, *Haliotis discus hannai*, veliger by the mucous trails of the juvenile and adult abalones. *Bull. Tohoku Reg. Fish. Res. Lab.* **43**, 29-36.
- Seki, T., & Kan-no, H. (1981b). Observations on the settlement and metamorphosis of the veliger of the Japanese abalone, *Haliotis discus hannai* Ino, Haliotidae, Gastropoda. *Bull. Tohoku Reg. Fish. Res. Lab.* **42**, 31-39.
- Shepherd, S.A. (1973). Studies on southern Australian abalone (genus *Haliotis*) I. Ecology of five sympatric species. *Aust. J. mar. Freshwater Res.* **24**, 217-257.
- Shepherd, S.A. (1986a). Movement of the Southern Australian abalone *Haliotis laevigata* in relation to crevice abundance. *Aust. J. Ecol.* **11**, 295-302.
- Shepherd, S.A. (1986b). Studies on southern Australian abalone (genus *Haliotis*) VII.

- Aggregative behaviour of *H. laevigata* in relation to spawning. *Mar. Biol.* **90**, 231-236.
- Shepherd, S.A., Clarkson P.S. & Turner, J.A. (1985). Studies on southern Australian abalone (genus *Haliotis*) V. Spawning, settlement and early growth of *H. scalaris*. *Trans. R. Soc. S. Aust.* **109**, 61-62.
- Shepherd, S.A. & Hearn W.S. (1983). Studies on southern Australian abalone (genus *Haliotis*). IV. Growth of *H. laevigata* and *H. ruber*. *Aust. J. mar. Freshwater Res.* **34**, 461-475.
- Shepherd, S.A., Kirkwood, G.P. & Sandland, R.L. (1982). Studies on Southern Australian abalone (genus *Haliotis*). III. Mortality of two exploited species. *Aust. J. Mar. Freshwater Res.* **33**, 265-272.
- Shepherd, S.A. & Laws, H.M. (1974). Studies on southern Australian abalone (genus *Haliotis*) II. Reproduction of five species. *Aust. J. mar. Freshwater Res.* **25**, 49-62.
- Shepherd, S.A. & Turner, J.A. (1985). Studies on southern Australian abalone (genus *Haliotis*). VI. Habitat preference, abundance and predators of juveniles. *J. exp. mar. Biol. Ecol.* **93**, 285-298.
- Shuto, T. (1983). Larval development and geographical distribution of the Indo-West Pacific *Murex*. *Bull. Mar. Sci.* **33**, 536-544.
- Sinclair, M. (1963). Studies on the Paua, *Haliotis iris* Martyn in the Wellington district, 1945-46. *Zool. Publ. Victoria Univ. Wellington*. No. **35**. 1-16.
- Sluczanowski, P.R. (1984). A management oriented model of an abalone fishery whose substocks are subject to pulse fishing. *Can. J. Fish. Aquat. Sci.* **41**, 1008-1014.
- Strathmann, R.R., Branscomb, E.S. & Vedder, K. (1981). Fatal errors in set as a cost of dispersal and the influence of intertidal flora on set of barnacles. *Oecologia* **48**, 13-18.
- Tanaka, Y. (1978). Swimming behaviour of the abalone larvae, *Nordotis gigantea* (Gmelin), in an outdoor tank. *Bull. Tokai Reg. Fish. Res. Lab.* **95**, 15-22.
- Tegner, M.J. (in press). The California abalone fishery: Production, ecological interactions, and prospects for the future. in '*Scientific approaches to the management of invertebrate stocks*.' (ed. Caddy, J.F.) (John Wiley and Sons)
- Tegner, M.J. & Butler, R.A. (1985a). Drift-tube study of the dispersal potential of green abalone (*Haliotis fulgens*) larvae in the southern California Bight:

- implications for recovery of depleted populations. *Mar. Ecol. Prog. Ser.* **26**, 73-84.
- Tegner, M.J. & Butler, R.A. (1985b). The survival and mortality of seeded and native red abalones, *Haliotis rufescens*, on the Palos Verdes Peninsula. *Calif. Fish Game* **71**, 150-163.
- Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* **25**, 1-45.
- Tomita, K., Tajima, K. & Kudo, K. (1977). Morphological observations of the veliger and the creeping larvae of an abalone, *Haliotis discus hannai*, from Rebun Island in the North-Western Hokkaido. *Sci. Rep. Hokkaido Fish. Exp. Stn* **19**, 13-18.
- Tong, L.J., Moss, G.A. & Illingworth, J. (1987). Enhancement of a natural population of the abalone, *Haliotis iris*, using cultured larvae. *Aquaculture* **62**, 67-72.
- Underwood, A.J. (1979). The ecology of intertidal gastropods. *Adv. mar. Biol.* **16**, 111-210.
- Vandermeulen, H. & DeWreede, R.E. (1986). The phenology, mortality, dispersal and canopy species interaction of *Colpomenia peregrina* (Sauv.) Hamel in British Columbia. *J. exp. mar. Biol. Ecol.* **99**, 31-47.
- Vincent, B., Vaillancourt, G. & LaFontaine, N. (1981). Cycle de developpement, croissance et production de *Pisidium amnicum* (Mollusca: Bivalvia) dans le Saint-Laurent (Quebec). *Can. J. Zool.* **59**, 2350-2359.
- Ward, T.J. (1986). Abalone biology and fisheries in Australia: a review of research. *Aust. Fish.Serv., Canberra, Aust. Fish. Pap. No. 86-12*. 1-36.
- Webber, H.H. & Giese, A.C. (1969). Reproductive cycle and gametogenesis in the black abalone *Haliotis cracheroidii* (Gastropoda: Prosobranchiata). *Mar. Biol.* **4**, 152-159.
- Winer, B.J. (1971). *Statistical principles in experimental design*. (McGraw-Hill Kogakusha, Tokyo), 1-907.
- Witherspoon, N.B. (1975). Sizes in the Tasmanian commercial catch of black-lip abalone (*Haliotis ruber*) - possible effects of changing habitat during growth. *Tas. Fish. Res.* **9**, 15-22.
- Yamaguchi, M. (1975). Estimating growth parameters from growth rate data. Problems with marine sedentary invertebrates. *Oecologia* **20**, 321-332.
- Yamaguchi, M. (1977). Shell growth and mortality rates in the coral reef gastropod *Cerithium nodulosum* in Pago Bay, Guam, Mariana Islands. *Mar. Biol.* **44**,

249-263.

- Yano, I. & Ogawa, Y. (1977). Effects of light, temperature and hydrostatic pressure on vertical distribution of abalone larvae, *Haliotis gigantea*. *Bull. Tokai Reg. Fish. Res. Lab.* **91**, 19-27.
- Yonge, C.M. (1947). The pallial organs of aspidobranch Gastropoda and their evolution throughout the Mollusca. *Phil. Trans. Roy. Soc. Ser. B.* **232**, 443-518.
- Young, C.M. & Chia, F.-S. (1982). Factors controlling spatial distribution of the sea cucumber *Psolus chitonoides*: Settling and post-settling behaviour. *Mar. Biol.* **69**, 195-205.

APPENDIX I

PUBLISHED MATERIAL FROM THIS

STUDY.

These articles have been removed for
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Prince, JD, Ford, WB, Use of anaesthetic to standardize efficiency in sampling abalone populations (Genus *Haliotis*; Mollusca : Gastropoda), Australian journal of marine and freshwater research, 1985, 36 (5), 701-706

Prince, JD, Sellers ,TL, Ford, WB, Talbot,SR, Experimental evidence for limited dispersal of haliotid larvae (genus *Haliotis*; Mollusca: Gastropoda), Journal of experimental marine biology and ecology, 1987, 103, (3), 243-263

Prince, JD, Sellers ,TL, Ford, WB, Talbot,SR, A method for ageing the abalone *Haliotis rubra* (Mollusca : Gastropoda), Australian journal of marine and freshwater research, 1988, 39 (2) 167-175

Prince, JD, Sellers ,TL, Ford, WB, Talbot,SR, Confirmation of a relationship between the localized abundance of breeding stock and recruitment for *Haliotis rubra* Leach (Mollusca: Gastropoda), Journal of experimental marine biology and ecology, 1988, 122, (2), 91-104

Prince, JD, Sellers ,TL, Ford, WB, Talbot,SR, Recruitment, growth, mortality and population structure in a southern Australian population of *Haliotis rubra* (Mollusca: Gastropoda), Marine biology, 1988, 100 (1), 75-82

APPENDIX II

A LISTING OF THE ITERATIVE MODEL FOR ANALYSING MULTIPLE RELEASE AND RECAPTURE DATA.

```
1 DIM FIRSTREL(5,5), NEWNUMB(5,5), SOUTHMOVNUMB(5,5),  
  EASTMOVNUMB(5,5)  
11 DIM NORTHMOVNUMB(5,5),SECREL(5,5), THIRDRREL(5,5), FOUREL(5,5),  
  MOVEINDEX(5,5)  
21 DIM PROFILE(4,9,5,9), RECAPTDAT(4,9,5,9),  
  RELEASE(5,5),WESTMOVNUMB(5,5)
```

```
REM *****INITIALIZE DATA*****
```

```
REM          Read in release data
```

```
REM Data read in order (2,2),(3,2),(4,2),(2,3),(3,3),(4,3),(2,4),(3,4),(4,4)
```

```
REM N.B. Abalone released in central 9 cells of a 25 cell grid.
```

```
REM FIRSTREL = Number released initially in each release grid cell.
```

```
DATA 35,35,54,48,42,38,47,75,29
```

```
FOR y = 2 TO 4: FOR x = 2 TO 4: READ FIRSTREL(x,y): NEXT: NEXT
```

```
REM Read in second release data SECREL = Number released in each grid cell during  
  second tagging period
```

```
DATA 35,60,98,43,28,29,52,20,21
```

```
FOR y = 2 TO 4: FOR x = 2 TO 4: READ SECREL(x,y): NEXT: NEXT
```

```
REM THIRDRREL = Number released in each grid cell during third tagging period
```

```
DATA 1,4,1,1,1,1,12,3,7
```

```
FOR y = 2 TO 4: FOR x = 2 TO 4: READ THIRDRREL(x,y): NEXT: NEXT
```

```
REM FOUREL = Number released in each grid cell during fourth tagging period
```

```
DATA 65,70,69,36,42,55,65,28,65
```

```
FOR y = 2 TO 4: FOR x = 2 TO 4: READ FOUREL(x,y): NEXT: NEXT
```

```
REM Read in the number of months from initial release to subsequent
```

```
REM recapture/release events. N.B. Initial release occurs at 0 months
```

```
REM and timing of final recapture must also be put down.
```

```
DATA 0,9,13,20,25
```

```
FOR T = 1 TO 5: READ MONTHS(T):NEXT
```

```
REM*****
```

```
REM          Read in recapture data
```

```

DATA 3,0,0,0,1,0,0,0,0
FOR i=1 TO 9: READ RECAPTDAT(1,1,1,i):NEXT
DATA 0,1,2,0,0,2,0,0,0
FOR i=1 TO 9:READ RECAPTDAT(1,2,1,i):NEXT
:
:   Read Data Statements
:
DATA 1,0,0,0,1,0,2,4,2
FOR i=1 TO 9:READ RECAPTDAT(4,8,5,i):NEXT
DATA 0,0,0,0,2,4,2,4,15
FOR i=1 TO 9: READ RECAPTDAT(4,9,5,i):NEXT

REM*****
REM           Read in model parameters

REM INITTL = Initial losses including tagging mortality and initial tag loss
REM SOUTHMOV = Proportion of animals in a grid moving into a shallower grid

REM NORTHMOV= Proportion moving deeper
REM EASTMOV= Depth neutral movement to east
REM WESTMOV= Depth neutral movement to west
REM CONTLOSS = Monthly rate of tag loss + mortality
REM CATCHABILITY = Probability of sighting abalone during a recapture search
REM KONSTANT & BEE = Constants for sighting probability model

100 INITTL = 0 : SOUTHMOV= .08: NORTHMOV=.03: WESTMOV = .04
110 EASTMOV = .075: CONTLOSS = .035: CATCHABILITY=.32
115 KONSTANT= .8 : BEE= 7
REM*****
REM           TEST PARAMETERS

FOR CONTLOSS = .14 TO .2 STEP .01
FOR INITTL= -.75 TO .15 STEP 1

FOR x = 1 TO 5: MOVEINDEX(x,1)=1.6 : NEXT
FOR x = 1 TO 5: MOVEINDEX(x,2)= 1.8: NEXT
FOR x = 1 TO 5: MOVEINDEX(x,3)=1.4: NEXT
FOR x = 1 TO 5: MOVEINDEX(x,4)=.5: NEXT
FOR x = 1 TO 5:MOVEINDEX(x,5)= .1: NEXT

SUMSQS = 0

```

```

FOR A= 1 TO 4: FOR B= 1 TO 9: FOR C= 1 TO 5: FOR d= 1 TO 9
PROFILE(A,B,C,d)=0
NEXT:NEXT:NEXT:NEXT

REM *****Begin model here*****

REM There are four release periods, this section sets up the model
REM for each release.
REM Determine which of four separate releases (r) are being modeled
FOR r = 1 TO 4
REM zero cell counter
CELL=0
REM Update FIRSTREL( ) to equal the appropriate number of animals
REM being released (subject to tagging mort & tag loss) plus the
REM previously released animals which have accumulated in the
REM particular grid from previous releases.

IF r=1 THEN FOR x=1 TO 5: FOR y=1 TO 5: RELEASE(x,y)=(FIRSTREL(x,y)-
((FIRSTREL(x,y))*(INITTL))):NEXT:NEXT
IF r = 2 THEN FOR x = 1 TO 5: FOR y = 1 TO 5: RELEASE(x,y) =
(SECREL(x,y)-((SECREL(x,y))*(INITTL))):NEXT:NEXT
IF r = 3 THEN FOR x = 1 TO 5: FOR y = 1 TO 5: RELEASE(x,y) =
(THIRDREL(x,y)-((THIRDREL(x,y))*(INITTL))):NEXT:NEXT
IF r = 4 THEN FOR x = 1 TO 5: FOR y = 1 TO 5: RELEASE(x,y) =
(FOUREL(x,y)-((FOUREL(x,y))*(INITTL))):NEXT:NEXT
REM*****
REM    Start tracking abs released in each cell
REM Determine which (x,y) cell is being modelled this loop in this release
FOR m = 2 TO 4: FOR l = 2 TO 4
REM establish a cell counter for use in data storage variable profile
CELL=CELL+1
REM*****
REM    zero all values for NEWNUMB before modelling a new release
FOR x=1 TO 5: FOR y=1 TO 5: NEWNUMB(x,y)=0: NEXT:NEXT
REM*****
REM    Add abs to the release cell cell
NEWNUMB(l,m)=RELEASE(l,m)
REM*****
REM    This Loop begins counting down the months within each release
REM    from time of release to final recapture
REM N.B. The number of abs in each cell is carried between months in the
REM    values of NEWNUMB( )

```

```

FOR T = (MONTHS(r)+1) TO MONTHS(5)
REM *****
REM Account for movement,mortality and tag loss
REM by modifying NEWNUMB( ) of each cell

FOR x = 1 TO 5: FOR y = 1 TO 5
REM account for mortality and tag loss
NEWNUMB(x,y)=NEWNUMB(x,y)-(NEWNUMB(x,y)*(CONTLOSS))
REM Estimate numbers moving in each direction
  SOUTHMOVNUMB(x,y)= (NEWNUMB(x,y)*SOUTHMOV) * Movindex(x,y)
  NORTHMOVNUMB(x,y)= (NEWNUMB(x,y)*NORTHMOV) * Movindex(x,y)
  EASTMOVNUMB(x,y)= (NEWNUMB(x,y)*EASTMOV) * Movindex(x,y)
  WESTMOVNUMB(x,y)= (NEWNUMB(x,y)*WESTMOV) * Movindex(x,y)
REM Account for movement out of and into cells
NEWNUMB(x,y)=NEWNUMB(x,y)-(SOUTHMOVNUMB(x,y) +
NORTHMOVNUMB(x,y) + (EASTMOVNUMB(x,y))+(WESTMOVNUMB(x,y)))
NEXT : NEXT:
REM Move abs. around the central grid cells
FOR x = 2 TO 4: FOR y = 2 TO 4
NEWNUMB(x,y)=(NEWNUMB(x,y))+(WESTMOVNUMB(x-1,y))+
  (EASTMOVNUMB(x+1,y))+(NORTHMOVNUMB(x,y-1))+
  (SOUTHMOVNUMB(x,y+1))
NEXT : NEXT
REM Move abs. around the fringe of the grid
REM This routine distributes abs to the fringe non-release cells (1,2-4) & (5,2-4)
FOR y = 2 TO 4
NEWNUMB(1,y)=NEWNUMB(1,y)+(EASTMOVNUMB(2,y))+
  (NORTHMOVNUMB(1,y-1))+(SOUTHMOVNUMB(1,y+1))
NEWNUMB(5,y)=NEWNUMB(5,y)+(WESTMOVNUMB(4,y))+
  (NORTHMOVNUMB(5,y-1))+(SOUTHMOVNUMB(5,y+1))
NEXT
REM This routine distributes abs to the fringe non-release cells (2-4,1) & (2-4,5)
FOR x= 2 TO 4
NEWNUMB(x,1)=NEWNUMB(x,1)+(SOUTHMOVNUMB(x,2))+
  (WESTMOVNUMB(x-1,1))+(EASTMOVNUMB(x+1,1))
NEWNUMB(x,5)=NEWNUMB(x,5)+(NORTHMOVNUMB(x,4))+
  (WESTMOVNUMB(x-1,5))+(EASTMOVNUMB(x+1,5))
NEXT
REM This routine distributes abs into the corners of the grid
NEWNUMB(1,1)=NEWNUMB(1,1)+EASTMOVNUMB(2,1)+
  SOUTHMOVNUMB(1,2)
NEWNUMB(1,5)=NEWNUMB(1,5)+EASTMOVNUMB(2,5)+
  NORTHMOVNUMB(1,4)

```

```

NEWNUMB(5,1)=NEWNUMB(5,1)+WESTMOVNUMB(4,1)+
SOUTHMOVNUMB(5,2)
NEWNUMB(5,5)=NEWNUMB(5,5)+WESTMOVNUMB(4,5)+
NORTHMOVNUMB(5,4)
REM *****
REM If the month is a recapture month save a density profile
IF T = 3 THEN RECAP = 1: GOSUB 1000
IF T = 9 THEN RECAP = 2: GOSUB 1000
IF T = 13 THEN RECAP = 3: GOSUB 1000
IF T = 20 THEN RECAP = 4: GOSUB 1000
IF T = 25 THEN RECAP = 5: GOSUB 1000
REM *****
REM          Goto next month
NEXT
REM *****
REM          Goto next cell to be modelled
NEXT: NEXT
REM *****
REM          Goto next release
NEXT
REM *****
REM          Least squares estimation routine
FOR d=1 TO 4: FOR C = 1 TO 9: FOR B = 1 TO 5: FOR A = 1 TO 9
DIFF = PROFILE(d,C,B,A)-RECAPDAT(d,C,B,A)
SQDIFF=DIFF*DIFF
SUMSQS = SUMSQS + SQDIFF
NEXT: NEXT: NEXT: NEXT
REM *****Next value for paramter*****
PRINT #1, USING "#####.#"; SUMSQS;
PRINT USING "#####.#"; SUMSQS;
NEXT
PRINT #1,
PRINT
NEXT
CLOSE#1
END

1000 FOR x= 2 TO 4: FOR y = 2 TO 4
REM Store distribution profile at the end of the recapture month N.B. catchability f
actor included in profile
REM This routine converts the grid co-ordinates into 9 numbered cells
REM (2,2)=1 (3,2)= 2 (4,2)=3 (2,3)=4 (3,3)=5 (4,3)=6 etc.

```

```
IF y=2 THEN convert = x-1
IF y>2 THEN convert = ((y-2)*3)+(x-1)
PROFILE(r,cell,recap,convert)=NEWNUMB(x,y)*(CATCHABILITY*(1+(bee*(EXP
    (-T/konstant))))))
NEXT: NEXT
RETURN
```

APPENDIX III

A LISTING OF THE ITERATIVE MODEL FOR ESTIMATING SIGHTING PROBABILITY.

```
FOR PROB = .2 TO .45 STEP .01
SUMSQS=0
REM*****

REM  1. PRESENT THRU 2 SEARCHES-RELEASED SEARCH 1

TOTAL=43
SEEN=(PROB)*TOTAL
NOTSEEN=(1-(PROB))*TOTAL
SUMSQS=((9-SEEN)*(9-SEEN))+((NOTSEEN-34)*(NOTSEEN-34))
REM*****

REM  2. PRESENT THRU 2 SEARCHES-RELEASED SEARCH 3

TOTAL=30
SEEN=(PROB)*TOTAL
NOTSEEN=(1-(PROB))*TOTAL
SUMSQS=SUMSQS+((14-SEEN)*(14-SEEN))+((NOTSEEN-16)*(NOTSEEN-16))
REM*****

REM  3. PRESENT THRU 3 SEARCHES-RELEASED SEARCH 1

TOTAL=29
SEENFIRST=((PROB)*(1-(PROB))*TOTAL)
SEENSECOND=((1-(PROB))*(PROB)*TOTAL)
SEENBOTH=((PROB)*PROB*TOTAL)
NOTSEEN=((1-(PROB))*(1-(PROB))*TOTAL)
SUMSQS=SUMSQS+((9-SEENFIRST)*(9-SEENFIRST))+
  ((5-SEENSECOND)*(5-SEENSECOND))+((3-SEENBOTH)*
  (3-SEENBOTH))+((12-NOTSEEN)*(12-NOTSEEN))
REM*****

REM  4. PRESENT THRU 3 SEARCHES-RELEASED SEARCH 3

TOTAL=24
SEENFIRST=((PROB)*(1-(PROB))*TOTAL)
```

```

SEENSECOND=((1-PROB)*(PROB)*TOTAL)
SEENBOTH=(PROB*PROB*TOTAL)
NOTSEEN=((1-PROB)*(1-PROB)*TOTAL)
SUMSQS=SUMSQS+((8-SEENFIRST)*(8-SEENFIRST))+
  ((3-SEENSECOND)*(3-SEENSECOND))+((4-SEENBOTH)*
  (4-SEENBOTH))+((9-NOTSEEN)*(9-NOTSEEN))
REM*****

REM 5. PRESENT THRU 4 SEARCHES-RELEASED SEARCH 1

TOTAL=10
REM *****SEEN ONE*****
SEENFIRST=((PROB)*(1-(PROB))*(1-(PROB))*TOTAL)
SEENSECOND=((1-(PROB))*(PROB)*(1-(PROB))*TOTAL)
SEENTHIRD=((1-(PROB))*(1-(PROB))*(PROB)*TOTAL)
REM *****SEEN TWO*****
SEENFIRSEC=((PROB)*(PROB)*(1-(PROB))*TOTAL)
SEENSECTHIR=((1-(PROB))*(PROB)*(PROB)*TOTAL)
SEENFIRSTHIR=((PROB)*(1-(PROB))*(PROB)*TOTAL)
REM *****SEEN ALL & NONE*****
SEENALL=((PROB)*(PROB)*(PROB)*TOTAL)
SEENNONE=((1-(PROB))*(1-(PROB))*(1-(PROB))*TOTAL)
REM*****SUM SQS*****
SUMSSEENONE=((1-SEENFIRST)*(1-SEENFIRST))+
  ((1-SEENSECOND)*(1-SEENSECOND))+((-SEENTHIRD)*
  (-SEENTHIRD))
SUMSSEENTWO=((1-SEENFIRSEC)*(1-SEENFIRSEC))+
  ((2-SEENSECTHIR)*(2-SEENSECTHIR))+((-SEENFIRSTHIR)*
  (-SEENFIRSTHIR))
SUMSQS=SUMSQS+((1-SEENALL)*(1-SEENALL))+((4-SEENNONE)*
  (4-SEENNONE))+SUMSSEENONE+SUMSSEENTWO

REM*****

REM 6. PRESENT THRU 5 SEARCHES-RELEASED SEARCH 1

TOTAL=8
REM *****SEEN ONE*****
SEENFIRST=((PROB)*(1-(PROB))*(1-(PROB))*(1-(PROB))*TOTAL)
SEENSECOND=((1-(PROB))*(PROB)*(1-(PROB))*(1-(PROB))*TOTAL)
SEENTHIRD=((1-(PROB))*(1-(PROB))*(PROB)*(1-(PROB))*TOTAL)
SEENFOURTH=((1-(PROB))*(1-(PROB))*(1-(PROB))*(PROB)*TOTAL)
REM *****SEEN TWO*****
SEENFIRSEC=((PROB)*(PROB)*(1-(PROB))*(1-(PROB))*TOTAL)

```



```

SEENSECTHIR=((1-(PROB))*(PROB)*(PROB)*(1-(PROB))*TOTAL)
SEENFIRSTHIR=((PROB)*(1-(PROB))*(PROB)*(1-(PROB))*TOTAL)
SEENTHIRFOURTH=(1-(PROB))*(1-(PROB))*(PROB)*(PROB)*TOTAL
SEENFIRSFOURTH=(PROB)*(1-(PROB))*(1-(PROB))*(PROB)*TOTAL
SEENSECFOURTH=(1-(PROB))*(PROB)*(1-(PROB))*(PROB)*TOTAL
REM *****SEEN THREE*****
SEENFIRSECTH=(PROB)*(PROB)*(PROB)*(1-(PROB))*TOTAL
SEENSECTHFOR=(1-(PROB))*(PROB)*(PROB)*(PROB)*TOTAL
SEENFIRSSECFOR=(PROB)*(PROB)*(1-(PROB))*(PROB)*TOTAL
SEENFIRSTHIRFOR=(PROB)*(1-(PROB))*(PROB)*(PROB)*TOTAL
REM *****SEEN ALL & NONE*****
SEENALL=((PROB)*(PROB)*PROB*PROB*TOTAL)
SEENNONE=((1-(PROB))*(1-(PROB))*(1-(PROB))*(1-(PROB))*TOTAL)
REM*****SUM SQS*****
SUMSSEENONE=((1-SEENFIRST)*(1-SEENFIRST))+
  ((SEENSECOND)*(SEENSECOND))+((SEENTHIRD)*(SEENTHIRD))+
  ((SEENFOURTH)*(SEENFOURTH))
SUMSSEENTWOA=((2-SEENFIRSEC)*(2-SEENFIRSEC))+
  ((SEENSECTHIR)*(SEENSECTHIR))+((SEENFIRSTHIR)+
  (SEENFIRSTHIR))+((1-SEENTHIRFOURTH)*(1-SEENTHIRFOURTH))
SUMSSEENTWOB=(SEENFIRSFOURTH*SEENFIRSFOURTH)+
  (SEENSECFOURTH*SEENSECFOURTH)
SUMSEENTHREE=(SEENFIRSECTH*SEENFIRSECTH)+
  (SEENSECTHFOR*SEENSECTHFOR)+(SEENFIRSSECFOR*
  SEENFIRSSECFOR)+(SEENFIRSTHIRFOR*SEENFIRSTHIRFOR)
SUMSQS=SUMSQS+((1-SEENALL)*(1-SEENALL))+((3-SEENNONE)*
  (3-SEENNONE))+SUMSSEENONE+SUMSSEENTWO

PRINT PROB, SUMSQS
NEXT
END

```

APPENDIX IV

LISTING FOR THE ABALONE POPULATION DYNAMICS MODEL.

```
CALL TEXTFONT(4)
CLS
FilNam$=FILES$(0,"NAME FOR OUTPUT FILE")
IF FilNam$="" THEN END
OPEN "O",#1,FilNam$
DIM n(25, 15), w(15), tzero(25), MOVEINDEX(25), density(25), s(15)
DIM stock(25), U(25), bhalf(25), pref(25), qual(25), opened(25)
DIM UPMOVNUMB(25,15), spawn(25), eff(25), catch(25),celldensity(25)
DIM DOWNMOVNUMB(25,15), NEUTMOVNUMB(25,15), cellcatch(25)
INPUT "no of years to simulate:"; NT:CLS
INPUT "annual effort:"; zzz:CLS
100 MOV = .24
REM ANNUAL MOVEMENT parameters
sold = .9
REM sold=survival of animals >11 years old
DATA .3,.4,.45,.50,.55,.60,.65,.70,.75,.80,.85,.87,.88,.89,.90
FOR a% = 1 TO 15: READ s(a%): NEXT
REM s(a%) = age dependent survival
REM establish growth parameters
DATA.0008,.043,.115,.207,.298,.371,.423,.459,.482,.497,.506,.512,.515,.517
FOR a% = 2 TO 15: READ w(a%): NEXT
REM Set up fishery parameters
aminlegal=8 'minimum age allowed to be caught
effort=0 ' effort in diving h
REM establish area specific characteristics
FOR i = 1 TO 25
    REM numbers in thousands
    n(i, 1) = 910
    FOR a% = 2 TO 15
        n(i, a%) = n(i, a% - 1) * s(a% - 1)
    NEXT
    n(i, 15) = n(i, 15) / (1 - sold)
    FOR a% = 8 TO 15
        rep = n(i, a%) * w(a%)
        spawn(i) = spawn(i) + rep
    REM spawn(i) is kgs/100 x 100 area
```

```

NEXT
    totalspawn = totalspawn + spawn(i)
NEXT
FOR ti = 0 TO NT
    REM model movement for each area and age group
    REM Estimate numbers moving in each direction
    FOR i=1 TO 25
        MOVEINDEX(i)=.239+(.106*spawn(i))
        IF MOVEINDEX(i) > 1 THEN MOVEINDEX(i) =1
    NEXT
    FOR a%= 8 TO 15
        FOR i=1 TO 25
            UPMOVNUMB(i,a%)= n(i,a%)*MOV
            DOWNMOVNUMB(i,a%)= (n(i,a%)*MOV)*MOVEINDEX(i)
            NEUTMOVNUMB(i,a%)= (n(i,a%)*MOV)*MOVEINDEX(i)
        NEXT
        REM MOVE ABS AROUND GRID..... CELLS 1,5,21,25
        n(1,a%)=n(1,a%)+NEUTMOVNUMB(2,a%)+NEUTMOVNUMB(6,a%)-
            2*NEUTMOVNUMB(1,a%)
        n(5,a%)=n(5,a%)+NEUTMOVNUMB(10,a%)+NEUTMOVNUMB(4,a%)-
            2*NEUTMOVNUMB(5,a%)
        n(21,a%)=n(21,a%)+NEUTMOVNUMB(16,a%)+
            NEUTMOVNUMB(22,a%)-2*NEUTMOVNUMB(21,a%)
        n(25,a%)=n(25,a%)+NEUTMOVNUMB(20,a%)+
            NEUTMOVNUMB(24,a%)-2*NEUTMOVNUMB(25,a%)
    REM CELLS 2-4
        n(2,a%)=n(2,a%)+NEUTMOVNUMB(1,a%)+NEUTMOVNUMB(3,a%)
            +DOWNMOVNUMB(7,a%)-2*NEUTMOVNUMB(2,a%)-
            UPMOVNUMB(2,a%)
        n(3,a%)=n(3,a%)+NEUTMOVNUMB(2,a%)+NEUTMOVNUMB(4,a%)+
            DOWNMOVNUMB(8,a%)-2*NEUTMOVNUMB(3,a%)-
            UPMOVNUMB(3,a%)
        n(4,a%)=n(4,a%)+NEUTMOVNUMB(3,a%)+NEUTMOVNUMB(5,a%)+
            DOWNMOVNUMB(9,a%)-2*NEUTMOVNUMB(4,a%)-
            UPMOVNUMB(4,a%)
    REM CELLS 22-24
        n(22,a%)=n(22,a%)+NEUTMOVNUMB(21,a%)+
            NEUTMOVNUMB(23,a%)+DOWNMOVNUMB(17,a%)-
            2*NEUTMOVNUMB(22,a%)-UPMOVNUMB(22,a%)
        n(23,a%)=n(23,a%)+NEUTMOVNUMB(22,a%)+
            NEUTMOVNUMB(24,a%)+DOWNMOVNUMB(18,a%)-
            2*NEUTMOVNUMB(23,a%)-UPMOVNUMB(23,a%)
        n(24,a%)=n(24,a%)+NEUTMOVNUMB(23,a%)+

```

```

    NEUTMOVNUMB(25,a%)+DOWNMOVNUMB(19,a%)-
    2*NEUTMOVNUMB(24,a%)-UPMOVNUMB(24,a%)
REM CELLS 6,11,16
    n(6,a%)=n(6,a%)+NEUTMOVNUMB(1,a%)+
    NEUTMOVNUMB(11,a%)+DOWNMOVNUMB(7,a%)-
    2*NEUTMOVNUMB(6,a%)-UPMOVNUMB(6,a%)
    n(11,a%)=n(11,a%)+NEUTMOVNUMB(6,a%)+
    NEUTMOVNUMB(16,a%)+DOWNMOVNUMB(12,a%)-
    2*NEUTMOVNUMB(11,a%)-UPMOVNUMB(11,a%)
    n(16,a%)=n(16,a%)+NEUTMOVNUMB(6,a%)+
    NEUTMOVNUMB(21,a%)+DOWNMOVNUMB(17,a%)-
    2*NEUTMOVNUMB(16,a%)-UPMOVNUMB(16,a%)
REM CELLS 10,15,20
    n(10,a%)=n(10,a%)+NEUTMOVNUMB(5,a%)+
    NEUTMOVNUMB(15,a%)+DOWNMOVNUMB(9,a%)-
    2*NEUTMOVNUMB(10,a%)-UPMOVNUMB(10,a%)
    n(15,a%)=n(15,a%)+NEUTMOVNUMB(10,a%)+
    NEUTMOVNUMB(20,a%)+DOWNMOVNUMB(14,a%)-
    2*NEUTMOVNUMB(15,a%)-UPMOVNUMB(15,a%)
    n(20,a%)=n(20,a%)+NEUTMOVNUMB(15,a%)+
    NEUTMOVNUMB(25,a%)+DOWNMOVNUMB(19,a%)-
    2*NEUTMOVNUMB(20,a%)-UPMOVNUMB(20,a%)
REM CELLS 7,9,17,19
    n(7,a%)=n(7,a%)+(UPMOVNUMB(2,a%)-DOWNMOVNUMB(7,a%))
    +(UPMOVNUMB(6,a%)-DOWNMOVNUMB(7,a%))+
    NEUTMOVNUMB(12,a%)+NEUTMOVNUMB(8,a%)-
    2*NEUTMOVNUMB(7,a%)
    n(17,a%)=n(17,a%)+(UPMOVNUMB(22,a%)-
    DOWNMOVNUMB(17,a%)+(UPMOVNUMB(16,a%)-
    DOWNMOVNUMB(17,a%))+NEUTMOVNUMB(12,a%)+
    NEUTMOVNUMB(18,a%)-2*NEUTMOVNUMB(17,a%)
    n(9,a%)=n(9,a%)+(UPMOVNUMB(4,a%)-
    DOWNMOVNUMB(9,a%)+(UPMOVNUMB(20,a%)-
    DOWNMOVNUMB(9,a%))+NEUTMOVNUMB(8,a%)+
    NEUTMOVNUMB(14,a%)-2*NEUTMOVNUMB(9,a%)
    n(19,a%)=n(19,a%)+(UPMOVNUMB(24,a%)-
    DOWNMOVNUMB(19,a%)+(UPMOVNUMB(20,a%)-
    DOWNMOVNUMB(19,a%))+NEUTMOVNUMB(14,a%)+
    NEUTMOVNUMB(18,a%)-2*NEUTMOVNUMB(19,a%)
REM CELLS 8,124, 18
    n(8,a%)=n(8,a%)+(UPMOVNUMB(3,a%)-
    DOWNMOVNUMB(8,a%)+(DOWNMOVNUMB(13,a%)-

```

```

        UPMOVNUMB(8,a%))+NEUTMOVNUMB(7,a%)+
        NEUTMOVNUMB(9,a%)-2*NEUTMOVNUMB(8,a%)
n(14,a%)=n(14,a%)+(UPMOVNUMB(15,a%)-
        DOWNMOVNUMB(14,a%))+(DOWNMOVNUMB(13,a%)-
        UPMOVNUMB(14,a%))+NEUTMOVNUMB(9,a%)+
        NEUTMOVNUMB(19,a%)-2*NEUTMOVNUMB(14,a%)
n(12,a%)=n(12,a%)+(UPMOVNUMB(11,a%)-
        DOWNMOVNUMB(12,a%))+(DOWNMOVNUMB(13,a%)-
        UPMOVNUMB(12,a%))+NEUTMOVNUMB(7,a%)+
        NEUTMOVNUMB(17,a%)-2*NEUTMOVNUMB(12,a%)
n(18,a%)=n(18,a%)+(UPMOVNUMB(23,a%)-
        DOWNMOVNUMB(18,a%))+(DOWNMOVNUMB(13,a%)-
        UPMOVNUMB(18,a%))+NEUTMOVNUMB(17,a%)+
        NEUTMOVNUMB(19,a%)-2*NEUTMOVNUMB(18,a%)
REM CENTRAL CELL 13
        n(13,a%)=n(13,a%)+UPMOVNUMB(12,a%)+UPMOVNUMB(8,a%)+
        UPMOVNUMB(18,a%)+UPMOVNUMB(14,a%)-
        4*DOWNMOVNUMB(13,a%)
NEXT
totalrecruits = 0
FOR i = 1 TO 25
REM age the animals and apply natural mortality
        n(i, 15) = sold * (n(i, 15) + n(i, 14))
        FOR a% = 14 TO 2 STEP -1
                n(i, a%) = s(a% - 1) * n(i, a% - 1)
        NEXT
'calculate total spawning effort (sum of mature nos * wts)
        rep=0: spawn (i)=0
        FOR a% = 8 TO 15
                rep = n(i, a%) * w(a%)
                spawn(i) = spawn(i) + rep
                REM spawn(i) is tonnes/100 x 100 area
        NEXT

REM spawn animals : divide by 2 for unproductive stock
REM stock recruit relationship
        IF spawn(i) <= 4.7 THEN
                n(i,1)=(1.884+(36.649*(spawn(i)*spawn(i)))-(18.115*spawn(i)))
        IF spawn(i) > 4.7 THEN
                n(i,1)=((650.1*spawn(i))-(41.2*(spawn(i)*spawn(i)))-1419.2)
        IF spawn(i) > 7.5 THEN
                n(i,1)=(520.5 + (137.2*spawn(i))-(7.23*(spawn(i)*spawn(i))))
        IF spawn(i) < .5 THEN n(i,1)=(4*spawn(i))

```

```

        IF i=13 THEN IF spawn(13) < 5 THEN
            n(13,1)=((spawn(13)/5)*800.9)
            totalrecruits = totalrecruits + n(i, 1)
        NEXT
' set up harvestable stock (kg/m2), totalstock= fishable tonnes for the entire area
totalstock=0
FOR i = 1 TO 25
    stock(i) = 0: density(i) = 0
    FOR a% = aminlegal TO 15
        density(i)=density(i)+(n(i,a%)/10)
    NEXT
NEXT
' effort and catch submodel here; sets cpue(i)=catch(i)/stock(i) for each area
' allocate effort over areas
totalpref = 1E-10
actualeffort = 0
effortblock = 5
FOR i = 1 TO 25: catch(i)=0: eff(i) = 0: celldensity(i) = density(i): NEXT
IF ti>10 THEN effort = zzz
FOR e% = 1 TO effort STEP effortblock
    bestqual=-999: bestcell=1
    FOR i = 1 TO 25
        qual(i) = celldensity(i)
    NEXT
    FOR i = 7 TO 9: qual(i) = qual(i)*1.2 : NEXT
    FOR i =12 TO 14: qual(i) = qual(i)*1.2 : NEXT
    FOR i =17 TO 19: qual(i) = qual(i)*1.2 : NEXT
    qual(13)=qual(13)*1.5
    FOR i = 1 TO 25
        IF qual(i)>bestqual THEN bestqual= qual(i): bestcell= i
    NEXT
    REM catch(i)= catch for each cell in number of abalone
    cellcatch(bestcell)=((celldensity(bestcell)*1128)/(1+(.0014*
        (celldensity(bestcell)*1128))))*effortblock
    catch(bestcell)=catch(bestcell)+cellcatch(bestcell)
    eff(bestcell)=eff(bestcell)+effortblock
    celldensity(bestcell)=celldensity(bestcell)-((cellcatch(bestcell)/10000))
NEXT
FOR i= 1 TO 25
    U(i)=1-(celldensity(i)/density(i))
    actualeffort = actualeffort + eff(i)

```

```

NEXT
'remove catch from age distribution for every area
REM totalcatch for entire area in tonnes
totalcatch = 0: totalstock = 0
FOR i = 1 TO 25
    stock(i)=0
    FOR a% = aminlegal TO 15
        totalcatch = totalcatch + n(i, a%) * w(a%) * U(i)
        REM totalcatch in tonnes
        n(i, a%) = n(i, a%) * (1 - U(i))
        stock(i) = stock(i) + n(i,a%) * w(a%)
    NEXT
    totalstock=totalstock + stock(i)
NEXT
totalspawn = 0
FOR i = 1 TO 25
    'calculate total spawning effort (sum of mature nos * wts)
    rep=0: spawn (i)=0
    FOR a% = 8 TO 15
        rep = n(i, a%) * w(a%)
        spawn(i) = spawn(i) + rep
        REM spawn(i) is tonnes/100 x 100 area
    NEXT
    totalspawn = totalspawn + spawn(i)
NEXT
REM cpue in kg/h
PRINT #1, USING "#####.##"; ti, totalstock, totalspawn, totalcatch,
REM NEXT year
NEXT
CLOSE #1
END

```